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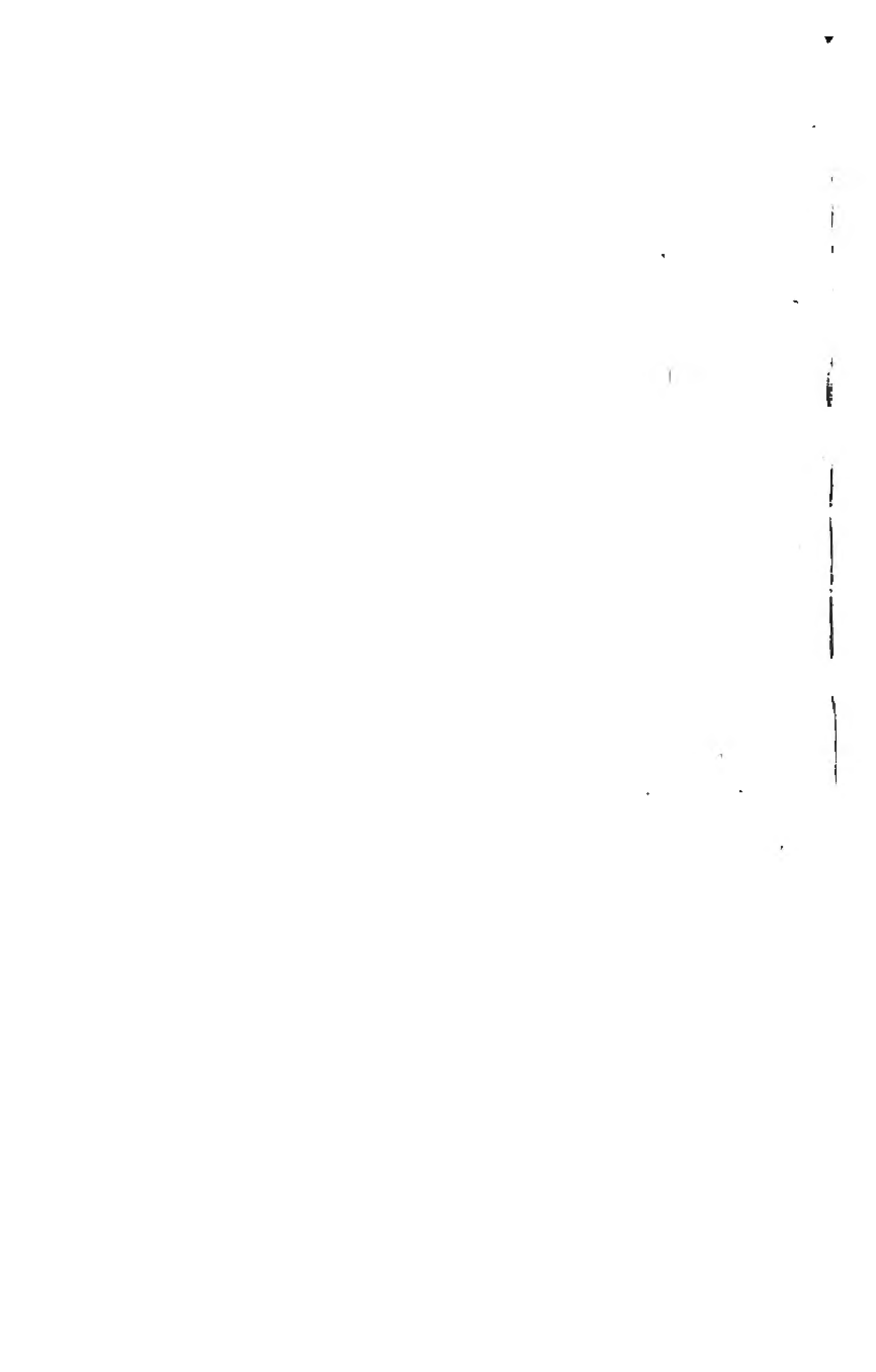
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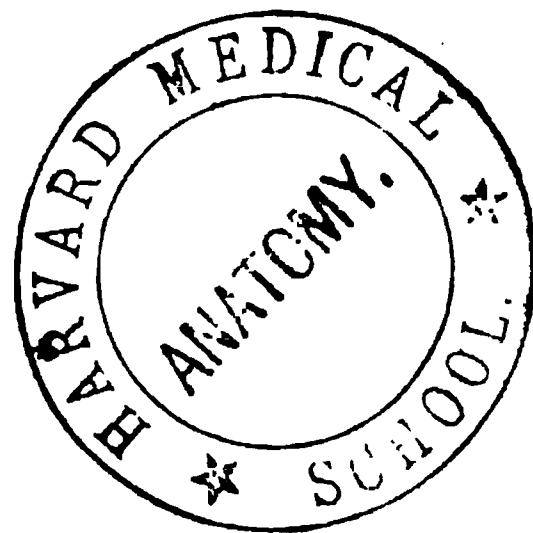
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Journal of Anatomy and Physiology.

A CONTRIBUTION TO THE STUDY OF THE MORPHOLOGY OF ADIPOSE TISSUE. By H. BATTY SHAW, M.D., *Assistant Physician to University College Hospital.*

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IN studying the literature dealing with the development of fat, it very soon becomes obvious that opinions in the past were very much divided, and two important views were held. On the one side there were observers who insisted on the belief that fat cells were developed from special cells set aside for the purpose of developing and storing fat; on the other, that fat cells were not specific structures, but that fat was stored up in cells which were everywhere widespread, and were constituents of connective tissue.

Todd and Bowman (1), writing in 1845, definitely state that adipose and areolar tissues should be looked upon as altogether distinct and independent tissues. In 1856 Kölliker described large polygonal cells with a finely granular but otherwise clear protoplasm occurring in the mesentery and around the kidneys in kittens one, two, or three days old; these cells were noticed a few days later to contain fat globules. Kölliker (2) considered that these polygonal cells were primitive, and that they formed definite structures which, from their appearance, should be considered as glands, and such he named them. Nearly thirty years later Kölliker (3) reaffirmed his views, stating that many fat lobules are produced from special kinds of connective tissue cells. He also asserts that the individual fat cells can be reconverted into connective tissue cells, and these again into fat cells.

In 1866 Czajewicz (4) published observations on fat formation, and was of the opinion that fat was laid down in connective tissue cells, but not in any special group of them, and that in cases of excessive feeding even the epithelial cells of the mesentery could be filled with fat globules. In 1870 Flemming (5) published two papers on the development of fat in the subcutaneous tissue and in the mesentery. In these two papers he has shown most conclusively that, in the situation examined, fat is deposited in simple fixed connective tissue cells. As a result of starvation, the fat was removed from these cells, and the original simple connective tissue cells were reproduced. In fig. 25 of plate viii. he shows a cell which has considerable resemblance to cells whose description will be given later.

In the same year Toldt (6) emphatically declared in favour of definite fat-forming organs. These he found in kittens and young rabbits under the skin, between the muscles, in the neck and around various joints and near the kidneys; the cells of these glands, before fat was formed within them, were very large, of variable form, and finely granular. He found the cells of the 'fat bodies' of frogs under conditions of insufficiency of food, to consist entirely of similar cells. The highly developed capillary system which formed a network through these 'fat glands,' especially attracted his attention.

In 1873, Klein (7), as a result of his investigations, considered that the fat lobules of the omentum and mesentery were transformed peri-lymphangeal lobules, and that, in agreement with Toldt, fatty tissue is a special form of glandular tissue. Waldeyer (8) concluded that the fat cells were formed according to Flemming's views, *i.e.* from simple fixed connective tissue cells, but that Toldt also was right in his assertion, that fat was laid down in special cells rich in protoplasm. In addition Waldeyer observed fat formation in the wandering 'plasma' cells which have since been known under his name. Toldt's views received further confirmation from Ranvier (9), whose observations were carried out in new-born rabbits and in calves. He noticed, as other observers had done, the close association of fat cells with blood-vessels, and that these cells near the vessels were more loaded with fat than those more remote—the latter, indeed, being quite free from fat. Ranvier inclined to the opinion that

each cell in question should be considered as a unicellular gland; he does not follow Toldt in naming the various fat accumulations 'fat glands.' In 1876 Flemming (10) again discussed the question. In his earlier papers he agreed with other observers that fat cells were closely associated with small blood-vessels, but in the later work he describes small groups of fat cells occurring, especially in young rodents, quite independent of vessels. He lays great stress upon the point, because earlier observers had quoted this close relationship of blood-vessels and cells as a strong support of the 'glandular' nature of the cells concerned. Flemming failed to find any sharp boundary between the fat cells and the other cells of the adjacent connective tissue.

Two years later an important paper was published by Löwe (11), who stated the three prevailing views as to the origin of fat droplets in cells. The first view was only mentioned to be dismissed for want of evidence, namely, that fat droplets were absorbed from the intestine and carried by the blood and implanted as such in certain cells. The second view was Flemming's 'impletion' theory; fat circulated in the blood as a watery solution, the blood then bathes certain connective tissue cells with the solution, and then these cells elaborated fat within themselves from the fluid supplied; if such cells began to atrophy, then the fat was again converted and carried off by the blood stream. The third theory was that of Toldt, the so-called 'ontogenetic' theory, by which it was supposed that certain special cells collected into glands had a special power of elaborating fat from the various materials of the blood plasma. He doubts Flemming's theory, because he says in the fat accumulations, described by others as glands, it is so very rare to be able to demonstrate connective tissue cells in the earliest stage of fat impletion. Löwe concludes that there are specific fat cells, and that they are primarily wandering cells.

Mr and Mrs Hoggan's (12) observations confirmed Flemming's views. Fat was not deposited in special fat cells or glands, but in branched cells, which they think, however, are wandering cells, whereas Flemming asserts that they are fixed. They studied fat formation as well as fat atrophy in cells of the broad ligament of rodents. In the former case they think fat is deposited in cells as single or many globules,

according to varying conditions of food supply, etc.; but that when fat cells atrophy, each fat globule does not break up into many globules, but remains one until it has quite disappeared.

In the same year Flemming's (13) fourth paper appeared. He still adheres to his former views, and shows that if an animal be starved sufficiently and sections be made of tissues existing in places where fat had originally been laid down, not only will the fat cells have disappeared, but the supporting capillary system will have atrophied too, and he figures atrophying capillaries; this, he says, is quite contrary to our conception of a gland, for the parenchyma should persist.

So far the review of the literature on the subject has been made with the object of getting clearer ideas as to the origin of fat cells. The careful observations made by Flemming in his four papers certainly establish the fact that fat is largely laid down in fixed branched connective tissue cells; it is possible that other cells are sometimes concerned in the process, but always to a much less degree, whether they be plasma cells described by Waldeyer, or the wandering cells described by Mr and Mrs Hoggan.

The next observers whose work remains to be reviewed, have called attention to the large polygonal, richly protoplasmic, cells first mentioned by Kölliker.

In 1883 Ehrmann (14) observed polygonal finely granular cells, which occasionally contained many fat globules, and he revives the name originally given to these cells by Ludwig, and calls them mulberry cells. Ehrmann is opposed to calling fat cells 'glandular,' and thinks they are probably wandering cells, as described by Waldeyer.

Bobritzky (15), in 1885, investigated fat formation in various mammals and arthropods, and thinks that fatty tissue develops out of a special element, and not from mere connective tissue cells; he describes rounded cells with granular protoplasm occurring in young embryos, in places in which eventually fatty tissues is laid down, and he says that these cells can be changed into wandering cells very similar in appearance to Waldeyer's plasma cells.

Poljakoff (16) has published observations on the subcutaneous tissues of white rats, and describes large spherical cells which in

some cases actually help to form the walls of the capillaries, and which, by a gradual transition, become fat-forming cells. He shows the effect of atrophy and inflammation upon these cells, but does not investigate the development. According to Poljakoff, Waldeyer's cells, Ranvier's flat cells, Ehrmann's mulberry cells and fat cells, are merely modifications of one embryonic cell found in connective tissue. According to Poljakoff, all the fat-containing cells are in close proximity to vessels; but this is in opposition to Flemming's observation above mentioned, namely, that fat cells can develop quite independently of proximity to vessel walls. Poljakoff says these cells may take on amoeboid movements.

Finally, in 1890 Metzner (17) published a paper, and inclines to the idea that there are special cells set apart for fat-formation, and that Flemming missed them by not examining early embryos. Metzner examined young animals and found a peculiar tissue in the axilla and thorax, and around the kidneys, which was quite free from fat, and consisted of large polygonal cells with granular protoplasm. He says these cells belong to connective tissue, but that they are not identical with connective tissue cells. He also starved animals, but found that developed fat could not be entirely got rid of, because the animals died before such a stage could be reached.

Despite all attempts to prove the existence of special cells set aside for the formation of fat, it must be admitted that the evidence is slight; no one, so far, has succeeded in getting rid of all the fat of the body of an animal and finding granular polygonal cells left massed together; all that is visible is connective tissue. In the examination of several cases of marasmus in infants, I have never been able to find such polygonal highly protoplasmic cells, nor in the development of fat in the body is it possible to demonstrate these large cells acting as precursors of fat-formation. The observations carried out and giving rise to this paper have been made on human fetuses from the fourth month till maturity, and on infants and older subjects of all ages.

In the adult human being adipose tissue has the ordinary characters ascribed to that tissue. It consists of large cells containing fat in the form of single globules, which are encircled

by a thin envelope of protoplasm, the presiding nucleus being dislocated from the centre of the cell to some spot at the periphery, giving rise to the well-known signet ring appearance. In the human embryo of about the fifth or sixth month, the fatty tissue present will be seen in the form of small yellow pellets beneath the skin; a few weeks later obvious accumulations are visible in the omentum, around the kidneys, in the axillæ, groins, under the parietal pleura, and in other places. In the case of the subcutaneous accumulation, the fat is deposited in connective tissue cells, usually as a single globule, which enlarges till it produces, by its growth, a much larger cell than the original; occasionally, however, the connective tissue cells are seen to possess more than one globule of fat, and there may be five or six; but eventually the same uniglobular fat cells are produced by the coalescence of the smaller globules. In the other sites mentioned, it is much more common for the fat to be deposited in the connective tissue cells in temporary drops, thus producing the appearance which Ludwig compared to that of a mulberry. These 'mulberry' fat cells, as well as those already mentioned as occurring in the subcutaneous tissue, tend eventually to assume the uniglobular form.

Towards the end of foetal life, a section of fat taken, say, from beneath the pleura, or from the axilla, will show many mulberry as well as uniglobular fat cells. Often there is visible a very well marked capillary system, the small vessels lying between adjacent cells. In addition, however, there will be seen cells whose characters are quite different from the fat cells amongst which they lie. They are rarely as large as the fat cells, but the nucleus is very similar; the great distinction, however, is the absence of fat globules; the protoplasm is finely granular, often is quite free from fat globules, even of the smallest dimensions, and is readily stainable. The contour of such cells is largely dependent upon the proximity of other cells; where they lie comparatively free from the pressure of adjacent cells, they are roughly spherical; often, however, so tight is the packing of the tissue in which they lie that they assume a polygonal form. After birth in the human subject, a very striking change takes place; in the case of two infants who died at the ages of two and three weeks respec-

tively, sections of the subpleural tissue, which in older subjects was found to consist of simple fat, showed that uniglobular fat cells were the exception; 'mulberry' fat cells were far less frequently met with, and the above-mentioned polygonal cells were visible in every field, free in many cases from any vestige of fat, occurring not singly but in irregular groups, which were interspersed amongst groups of cells possessed of fat globules, more or less 'mulberry' in form. The protoplasm of these cells was extremely abundant, and a first glance of the tissue

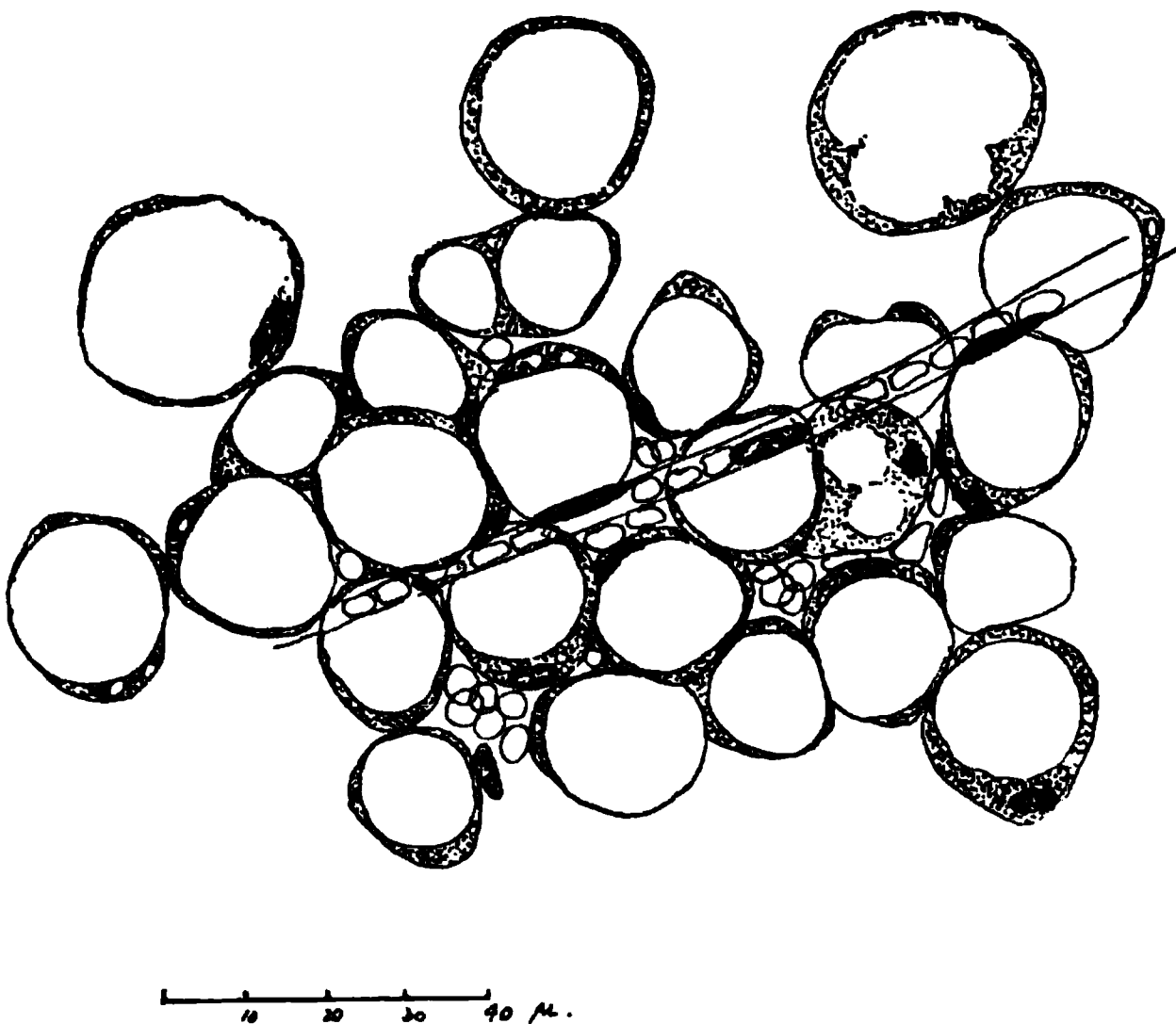


FIG. 1.—Section taken from subpleural tissue of a foetus of the seventh month.
Most cells in this drawing show single globules of fat.

would suggest a likeness to a layer of squamous epithelium, so extensive is the area of protoplasm as compared with the size of the nucleus. A closer observation, however, would at once disclose the fact that here, as in other sections of adipose tissue examined, there is an abundant capillary network; the capillaries seem to cut notches in the contour of the cells occupying a position between adjacent cells, very much like that of the bile canaliculi between the liver cells. In this study it was a matter of great good fortune that the cause of death in the two subjects first described was asphyxia from overlying: the result

has been that the minutest capillaries are found packed full of red corpuscles, which so readily take up the eosin stain.

In examining older infants than the last two, a reversion is met with to the type of tissue seen in foetuses of six, seven, eight, or nine months of age, *i.e.* there is an abundance of uni- and multi-globular fat cells, and only here and there can a 'pleo-protoplasmic' cell be discovered. Subjects of six years and older show the ordinary uniglobular fat cells.



FIG. 2.—Section taken from subpleural tissue of a foetus of the ninth month. No simple fat cells visible; most are 'mulberry' like; one is seen quite free from fat.

The illustrations shown in this description are taken from sections of subpleural tissue, as that is the tissue which was preserved with the greatest care in the first case; unfortunately, samples of fat were not taken from other localities of the same individuals, to see whether similar changes went on in all parts. In many cases perirenal and axillary fat have been examined, and show, generally, changes very similar to that above described.

Seeing that the above change in fat cells occurs shortly after birth, and in turn gives place to a further development of fat cells in a week or two, it may well be thought to be due to a

sudden call upon the stored fat, incident upon the passage from



FIG. 3.—Section taken from the subpleural tissue of an infant two weeks old. This sketch shows the cells in their 'pleo-protoplasmic' condition; also abundant capillary network with nuclei of capillary epithelium. Some cells are 'mulberry' like in appearance.

intra-uterine to an independent existence. That this is not so,

however, is proved by the fact that in some of the lower mammals a similar condition of fat cells is met with at, or even before birth, the 'pleo-protoplasmic' condition being found in fat in all localities, though not necessarily to an equal degree in each locality. Again, it may be thought that all fat cells, when

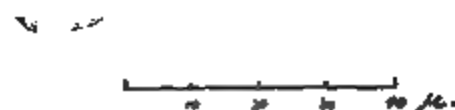
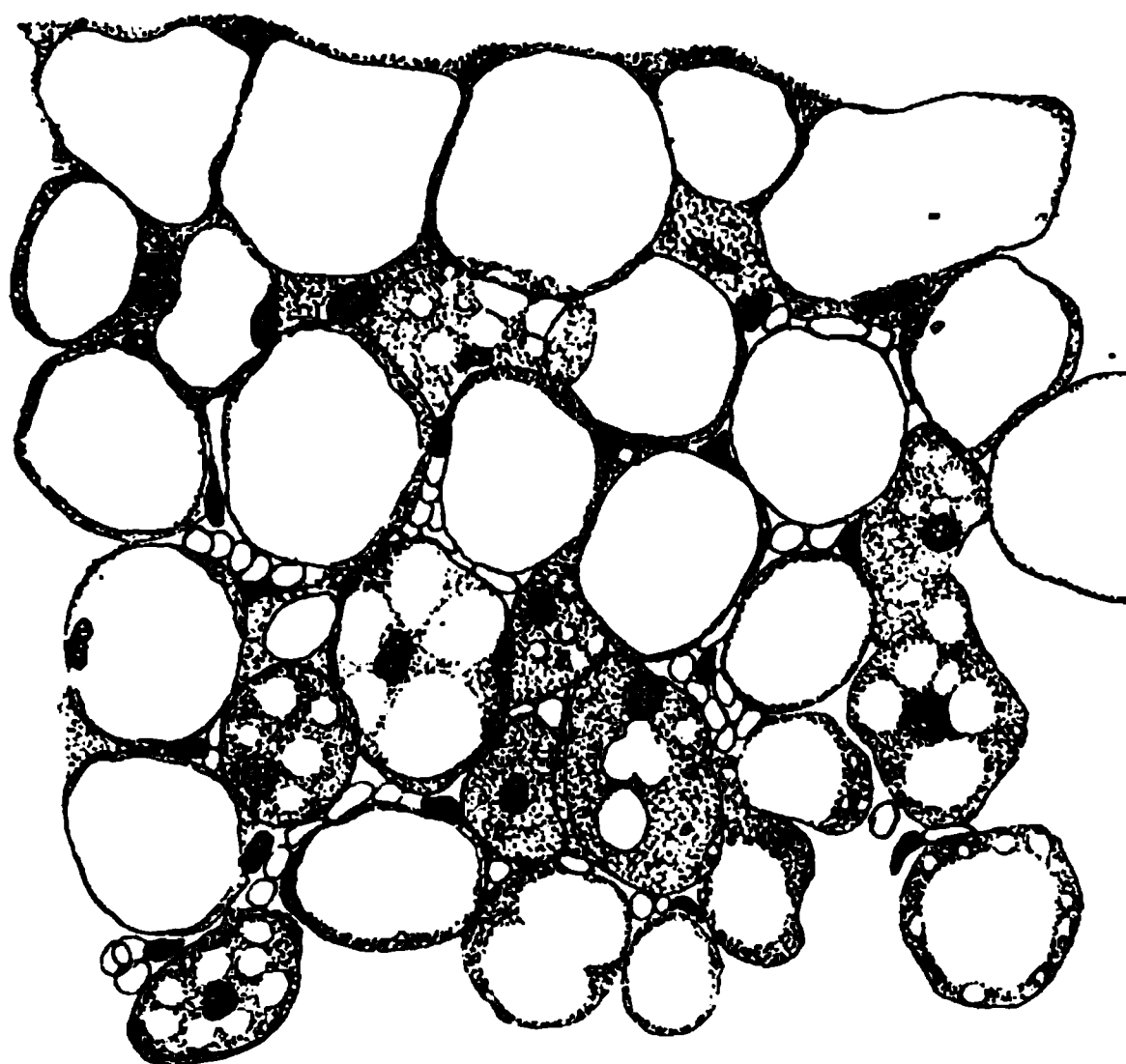


FIG. 4.—Section taken from the subpleural tissue of an infant three weeks old.
The appearance is the same as that of infant two weeks old.

deprived of their fat globules, would assume the appearance met with in the young infants above described, but the objections to this view are, that in the numerous starvation experiments that have been made, similar cells have not been met with; the starvation not only removes the fat, but the protoplasm as well, and the cells rapidly assume the characters of connective

tissue cells; further, in studying the development of fat, besides being convinced that Flemming is right as to the beginning of fat formation, by the development of fat globules in connective tissue cells, it is a fact that the pleo-protoplasmic stage above referred to is never met with; it is not a necessity for the deposit of fat in a cell that such cell should be abundantly supplied with protoplasm; in the omentum, for example, fat may be seen



— 10 20 30 40 μ .

FIG. 5.—Section taken from subpleural tissue of an infant eleven months old. Shows many simple fat cells, others of the 'mulberry' type; one in the lower part quite free from fat.

deposited as two or three globules in cells whose protoplasm is quite scanty.

The methods adopted in this study have been purely histological; the fixation of the tissues in Flemming's solution has repeatedly proved that the globules under examination were fatty. Exceptions, however, were met with, *e.g.* some globules appeared to be other than fatty, as they did not show the same effect at all; other globules showed an incomplete effect,

possibly due to the transition to fat. With further investigation, it may be possible to make out some chemical differences in these cells whilst they are in this stage of metamorphosis. It is quite easy in the dissection of the axilla of a new-born child, to separate fully developed fat from fat showing this change—the latter tissue looks more pink, appears firmer, and does not adhere to the scalpel as fat does.

In conclusion, the above study points to the suggestion that much of the discussion as to the origin of fat has been brought about by the fact that Kölliker, and those who accepted his views, had not traced fat to a sufficiently early period of life. Had they done so they must have accepted Flemming's statement that there were no special 'fat glands,' and that all fat commenced as deposits in connective tissue cells. Kölliker, struck with the appearance of fat cells such as has been described above, looked upon the appearance as that of a gland, instead of considering it as merely a metamorphosis occurring in the fat of the body reaching its maximum at or before birth in some quadrupeds, and in the infants above-mentioned some two or three weeks after birth.

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**STRUCTURE OF THE LEFT AURICULO-VENTRICULAR
VALVE IN BIRDS.** By A. HODGKINSON, B.Sc. Vict.,
Owens College, Manchester.

WHILE working in the zoological laboratory at Owens College, I noticed that the left auriculo-ventricular valve of the pigeon I was dissecting did not agree with the description given in the text-book. I therefore examined the hearts of several pigeons and other birds, with the results recorded in this paper.

I have to accord my thanks to Professor Hickson and Dr

ALC	LC
MC	B
AMF	MP
	MP

FIG. 1.—Heart of a Turkey. The left wall of the left ventricle has been removed so as to show the auricular-ventricular valve. *A.L.C.*, antero-lateral cusp. *P.L.C.*, postero-lateral cusp. *M.C.*, median cusp. *F.B.*, fibrous band. *A.M.P.*, anterior muscular papilla. *L.M.P.*, lateral muscular papilla. *P.M.P.*, posterior muscular papilla.

Gamble for suggestions and assistance in working out this point.

The frequent statement in text-books that the left auriculo-ventricular opening in birds is guarded by a mitral valve formed of two membranous flaps, is, I think, not strictly correct. Having dissected several hearts with regard to this valve, and finding that in each case it consisted of three flaps and not two, I

turned to the literature on the subject, and found that the various statements differed with regard to the number of flaps or cusps.

Cuvier, in his *Leçons D'anatomie Comparée*, describes it as follows:—"L'embouchure de l'oreillete dans ce ventricule est entourée d'un voile membraneux parfaitement semblable à la valvule mitrale des mammifères partagé en deux portions comme cette valvule." Owen, in his *Anatomy of Vertebrates*, describes it as being formed by two membranous folds which correspond to the mitral valve of mammals. It would thus

ALC	LC
	IC
AMP	MP
	MP

FIG. 2.—Heart of a Goose. The same dissection has been made as in fig. 1; lettering also the same.

appear that several of our English authors who have described this structure have based their description on the statements of Cuvier and Owen, for they describe it as a mitral valve consisting of two portions. On the other hand, F. Meckel, Carl Röse, and Wiedersheim, in the third edition of his *Comparative Anatomy of Vertebrates* (translated by W. N. Parker), state that it is formed of three membranous folds. There is still a third statement, namely, that the left atrio-ventricular valve in birds is formed of two or three flaps (*Dictionary of Birds*, by A. Newton, assisted by H. Gadow). Further dissections were then made in the hope of getting at the true state of affairs.

It may be of value here to give a few figures of this structure, as I have been unable to find any in the papers or text-books which deal with this subject. The hearts of the following birds were dissected:—pigeon (14), hen (27), turkey (3), grouse (3), pheasant (1), partridge (6), sparrow (1), blackbird (1), duck (3), goose (3), and cassowary (1), the total number of hearts being sixty-three; and, without exception, each left atrio-ventricular valve was found to consist of three well-marked cusps. Carl Röse, in a paper on the comparative anatomy of the hearts of vertebrates, speaks of this valve as being formed of a median and two lateral cusps. Of these two lateral cusps I propose to

	LMP
ALC	PLC
AMP	MC
	PMP

FIG. 3.—Heart of a Pigeon. The same dissection has been made as in the other two hearts, but the lateral muscular papilla has been turned up so as to give a better view of the median cusp. Lettering as before.

call the anterior the antero-lateral, and the posterior the postero-lateral. The median cusp is generally the largest, closing about half the area of the opening. In the heart of the cassowary which I possess, it is, however, about the same size as the other two cusps, consequently closing about a third of the opening only. It is situated between the aortic and left atrio-ventricular openings, being parallel with the ventricular septum, occupying, therefore, the same position as does the anterior or median cusp of the mammalian mitral valve, to which it corresponds.

The antero-lateral cusp is much smaller, and closes about a quarter of the opening; it is situated external and slightly

anterior to the opening. The postero-lateral cusp is about the same size as the antero-lateral, and is situated external and slightly posterior to the opening.

In the heart of the cassowary referred to, these two cusps are relatively larger than in the hearts of the other birds examined. In my specimen the three cusps are about equal in size.

These lateral cusps have the position of the posterior cusp of the mammalian mitral valve, to which they may be said to correspond.

There are generally three muscoli papillares—an anterior, posterior, and a lateral. They are so situated that they alternate with the cusps of the valve, and send chordæ tendineæ to

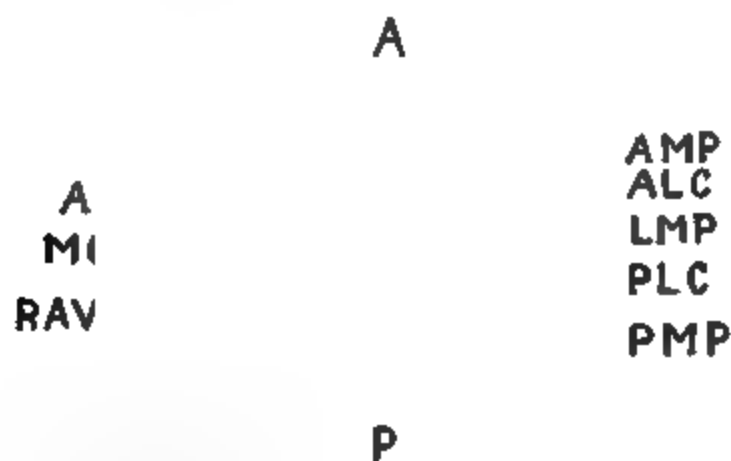


FIG. 4.—Heart of a Pigeon, showing the auriculo-ventricular valves from below. The observer is supposed to be looking up into the ventricles, the apex and greater part of which have been removed. *A.O.*, aortic orifice. *R.A.V.V.*, right auriculo-ventricular valve. *A.*, anterior. *P.*, posterior. The rest of the lettering as in fig. 1.

the intervals between the cusps into the edges and ventricular surfaces of which they are inserted.

With regard to the size of these papillæ, it may be stated that, as a rule, the lateral is the largest, the anterior comes next, and the posterior last.

The lateral papilla in many cases sends up a strong band of muscular fibres which are inserted into the ventricular wall and valve where these two structures meet. This band of fibres is entirely absent in the hearts of the ducks, geese, partridges and cassowary which were examined; it was also not constant in the other hearts.

There is a certain similarity between this tricuspid valve of

birds and the mitral valve of mammals. The resemblance is more striking in the hearts of those birds, such as the goose, in which the lateral cusps have a tendency to fuse. If the lateral papilla be removed, we get a mitral type of valve such as that of the mammal.

Carl Röse has drawn attention to the striking resemblance between the left atrio-ventricular valve of the bird on the one hand, and that of monotremes on the other; this valve in the latter, as he points out, having three cusps and three muscoli papillares. The mitral valve of the marsupial he considers to have been produced from the monotreme type by a fusion of the lateral cusps and the loss of the lateral musculus papillaris.

It is interesting to note that Professor Ray Lankester compares the right auriculo-ventricular valvular apparatus of monotremes to the corresponding structure in birds.

Thus, I think we may say that the auriculo-ventricular valves of the mammal have, in their evolution, passed through a condition closely similar to that found in birds.

Meckel records that in one out of the three ostrich hearts which he examined, he found a mitral valve; the other two had tricuspid valves.

From my dissections I conclude that the left auriculo-ventricular valve in birds is formed of three cusps, and is therefore of the tricuspid type. If there are other cases besides that of Meckel's ostrich in which the three cusps are replaced by two, these I should consider to be variations from the prevalent type.

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ON THE DEVELOPMENT OF THE RENAL-PORTALS
AND FATE OF THE POSTERIOR CARDINAL VEINS
IN THE FROG. By THOMAS W. SHORE, M.D., B.Sc.,
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Bartholomew's Hospital and College.*

(From the Biological Laboratory of St Bartholomew's Hospital.)

MY attention was directed to the subject of the development of the renal-portal veins and fate of the posterior cardinals in the frog by a case of an abnormal renal-portal vein which was described and figured in this Journal a year or so ago.¹ The specimen in question seemed to me to throw some doubt on the currently accepted view of the development of these veins, and on the relation which the renal-portals have to the posterior cardinals. In the paper referred to I expressed the opinion that the renal-portals are developed from a portion of the posterior cardinals. According to currently accepted views,² the hinder parts of the two posterior cardinals become united together, and the median vessel thus formed is joined by the anterior part of the post-caval, which arises as a distinct vessel independently of the posterior cardinals, and can be traced backwards from the sinus venosus along the left dorsal surface of the liver to the anterior end of the developing mesonephros, where it becomes continuous with the two cardinals, which form its posterior continuation. According to Marshall, the renal portal veins are formed "by longitudinal anastomotic communications between the transverse or vertebral veins of the hinder part of the body; they are joined posteriorly by the iliac veins, and with these form the afferent renal system of veins."

In a second paper,³ in which I described another case of abnormal arrangement of the renal-portal vein in the frog, I

¹ Shore, "Unusual Arrangement of the Renal Portal Vein in the Frog," *Journal of Anat. and Phys.*, vol. xiv., N.S., p. 398.

² Marshall, *Vertebrate Embryology*, 1893, p. 184.

³ Shore, "Abnormal Veins in the Frog," *Journal of Anat. and Phys.*, vol. xv., N.S., p. 323.

stated that my investigation of frog-tadpoles had led me to the conclusion that the hinder section of the post-caval is formed from a part of the posterior cardinals, and that another part of them is connected with the development of the renal-portals. The present communication is a description of my investigations, and a fuller statement of their results.

I. *Methods of Work.*—My methods of work have been simple. Frog-tadpoles are easily obtained and reared at the breeding season in spring. They were taken at different stages up to the tailed-frog stage. Greatest numbers were examined of the earlier stages. The tadpoles were killed and hardened—some in mercuric chloride solution, others in picric acid, and some simply in alcohol. After hardening, they were mostly stained in bulk, it being found by experience desirable to avoid all unnecessary manipulation after the sections were cut. The stains employed were chiefly picrocarmine, borax carmine, and alum-cochineal. The first is very useful, as it enables one to pick out more certainly the course of the small blood channels by staining the protoplasm of the blood corpuscles yellow. After staining, the tadpoles were dehydrated, soaked in benzole or turpentine, and embedded in paraffin. They were cut in ribbons by the rocking microtome. Most of the series are transverse sections, but of each stage some longitudinal sagittal sections were cut, as well as a few horizontal longitudinal ones. The following are the stages which were studied:—(a) tadpoles of about 9 to 10 mm. length, (b) those of about 11 to 12 mm., (c) tadpoles of 14 to 15 mm., (d) tadpoles of 18 mm., (e) those about 20 mm. long, (f) those about 23 mm. long, (g) tadpoles of 25 mm., (h) a few of 30 mm. and 35 mm. length, (i) one or two older ones up to metamorphosis, (j) one or two tailed frogs.

The sections are mostly about 50 μ in thickness, but some are rather thicker.

II. *Arrangement of the Posterior Cardinals in a 10 mm. tadpole.*—Before dealing with the changes which take place in the arrangement and relations of the posterior cardinals as the tadpole passes to adult life, it is necessary to describe the position and connections of these veins at a stage when they have become

definitely established, and when they are in what may be regarded as their primary condition. Such a typical condition is found in tadpoles of from 9 to 10 mm. in length. If a series of transverse sections of a 10 mm. tadpole be examined, the whole course of the posterior cardinals can be traced. Beginning with the tail region, we find throughout the greater part of this organ, indeed the whole except quite the hinder end, there is a single median vein lying ventral to, but not immediately in contact with, the caudal continuation of the dorsal aorta. Its walls are thin and are made up of a single layer of flattened epithelial

--- n.c.

.... n.

.... ao.

.... v.c.

FIG. 1.—Transverse section of the middle of tail of a 10 mm. tadpole. n.c., central nerve cord; n., notochord; ao., aorta; v.c., caudal vein.

cells only. It lies in the midst of loosely-arranged mesoblast cells bounded laterally by the muscle somites. A typical section from near the root of the tail is shown in fig. 1, in which the position of the vein is well shown (v.c.). This is the caudal vein, and is by Balfour¹ regarded as a part of the ancestral sub-intestinal vein of fishes. Working forwards, we trace the caudal vein into the posterior end of the trunk, where it lies dorsally to the cloaca, and there divides into two vessels which pass forwards side by side ventral to the dorsal aorta. These are the hindermost extremities of the posterior cardinals, which may therefore be described as arising by the bifurcation

¹ Balfour, *Comparative Embryology*, vol. ii., 1881, p. 537.

of the caudal vein. Traced forwards, these next come into relation with the hinder ends of the segmental ducts, each of which at its termination in the cloaca is placed ventrally to the corresponding cardinal vein. A drawing of a section at the junction of the segmental ducts with the cloaca is given in fig. 2, which shows very well the relations of the ducts (*s.d.*), cloaca (*cl.*), and cardinal veins (*v.p.c.*) to each other.

From this point the posterior cardinals run forwards parallel to one another throughout the whole of the hinder part of the trunk, lying in close relation to the segmental ducts, which in most of their course appear to be partly, and in places wholly,

-- *n.c.*
 -- *n.*
 --- *ao.*
 ---- *v.p.c.*
 --- *s.d.*
 *cl.*
 --- *coel.*

FIG. 2.—Transverse section of a 10 mm. tadpole passing through the termination of the segmental ducts in the cloaca. *n.c.*, central nerve cord; *n.*, notochord; *ao.*, aorta; *v.p.c.*, posterior cardinal vein; *s.d.*, segmental duct; *cl.*, cloaca; *coel.*, coelom.

surrounded by the veins; the thin layer of flattened epithelial cells which form the vein-wall being in contact with the outer end of the cells of the segmental ducts. The greater part of the vein on each side, however, lies internal to the corresponding duct, and the whole, veins and ducts, form a pair of broad ridges—the urinary ridges—with the dorsal mesentery arising in the middle line between them. These points are shown in fig. 3, which is a drawing of a section about forty in front

of that shown in fig. 2. In this part of the course of the cardinals, the first traces of the nephridia of the mesonephros may be made out, but since their origin can be better studied in a tadpole a little older, the description of them will be given later. At intervals the cardinal veins receive on their outer aspects a few small somatic veins from the dorsal body wall. These are somewhat irregular in their disposition, but are roughly metameric.

At about the level of the lower limit of the liver, the posterior cardinals begin to separate from each other and diverge from the middle line, each passing obliquely outwards towards the very prominent corresponding pronephros. Here the segmental ducts are completely surrounded by the vein. This is shown in



FIG. 3.—Transverse section of a 10 mm. tadpole passing through the mesonephric parts of the cardinals. *n.c.*, central nerve cord; *n.*, notochord; *aa.*, aorta; *s.d.*, segmental duct; *v.p.c.*, posterior cardinal vein.

fig. 4, *v.p.c.* and *s.d.* This oblique, indeed almost transverse, part of the cardinal can be traced through a few sections only, for it very soon reaches the pronephros. Around the pronephros, the vein forms an extensive vascular network, penetrating into the organ and surrounding the individual tubules of which it is built up. The nephridia are much coiled, and the flattened cells of the vein-wall are reflected over the surface of each tubule following its course accurately as an outer covering of cells, which alone separate the blood of the vein from the proper walls of the nephridia. The vein has, indeed, a sinus-like character, the nephridia having grown into it, invaginating its

wall as a reflection over themselves, so subdividing it into a network of irregular channels. A section through the middle of the pronephros showing these points is figured in fig. 5. On the right side of the drawing (the animal's left) one of the pronephric nephrostomes, which can easily be recognised by the pigmentation of their cells, is shown; and the glomerulus of the pronephros is seen on both sides, growing out from the aortæ, which are cut just in front of their union to form the median dorsal aorta. The pronephros extends forwards as far



FIG. 4.—Transverse section of a 10 mm. tadpole passing through the oblique parts of the cardinals. *n.c.*, central nerve cord; *n.*, notochord; *ao.*, aorta; *v.p.c.*, posterior cardinal vein; *s.d.*, segmental duct; *l.l.*, *l.r.*, left and right lung; *li.*, liver; *h.d.*, bile duct; *v.h.p.*, hepatic portal vein.

as the anterior limit of the posterior cardinal, so that in the whole of the rest of its course, to where it becomes continuous with the Cuvierian vein, it has the sinus-like character just described. A drawing of its anterior termination is given in fig. 6, in which its relations to the Cuvierian vein and sinus venosus, as well as the junction of the vitelline vein with the sinus, are shown. The section also shows the terminations, near the union of the posterior cardinal and Cuvierian veins, of the right and left lateral veins (*v.l.r.* and *v.l.l.*), which arise from

a vascular network on the anterior part of ventral body wall. These represent the lateral veins of Elasmobranch fishes, and one or both of them subsequently forms the front end of the anterior abdominal vein of the adult frog.

In the above account the important points to note are—(1) the posterior origin of the cardinals from the caudal; (2) the subdivision of each cardinal into a straight posterior section which, since the mesonephros subsequently forms here, we may call the *mesonephric part*; a sinus-like anterior portion or *pro-*



FIG. 5.—Transverse section of a 10 mm. tadpole passing through the pronephric parts of the cardinals. n.c., central nerve cord; n., notochord; aa., aorta; pr.n., pronephros; n.st., nephrostome; g., glomerulus; s.d., segmental duct; l.l., left lung; li., liver; v.p.c., posterior cardinal vein; v.v., vitelline vein.

nephric part; and an *oblique part* connecting the other two; (3) the sinus-like character of the pronephric parts, and the very intimate relations of the veins to the pronephroi which are embedded in great venous sinuses. A similar sinus-like arrangement is beginning in the mesonephric parts where the segmental ducts are already partly invaginated into them.

III. *Posterior Cardinals in a 12-13 mm. tadpole.*—In tadpoles about 12-13 mm. long the general disposition of the posterior

cardinals is very similar to that of a 10 mm. tadpole. The most important change is that the first trace of what will become the front part of the post-caval vein has been formed and has acquired a connection with the *right* posterior cardinal.

In a 9 or 10 mm. tadpole the venous connection between the liver and the sinus venosus is effected by the proximal parts of the original vitelline veins which have become united into a common trunk. The common vitelline vein is continued distally into the sinus-like capillary system of the liver. The vitelline

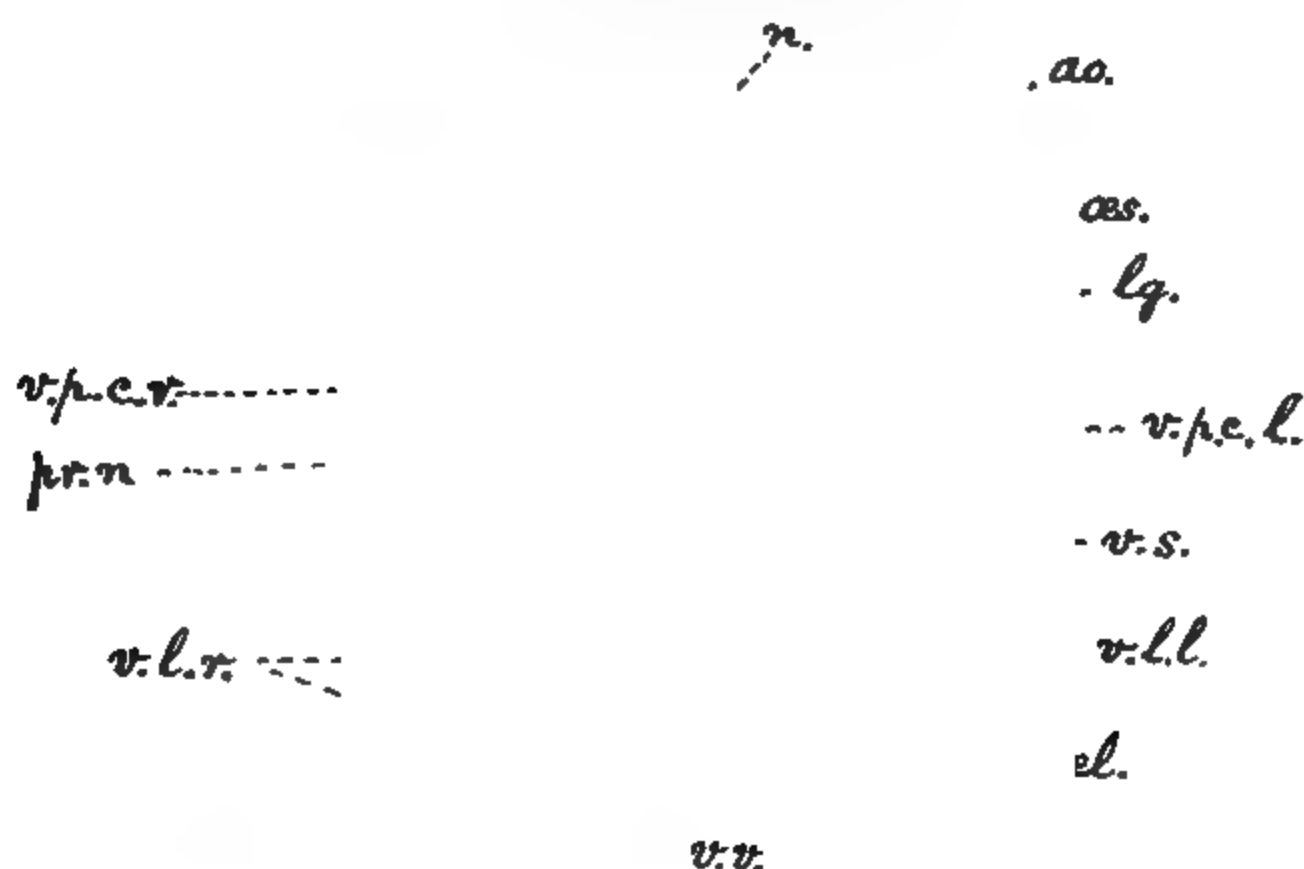


FIG. 6.—Transverse section of a 10 mm. tadpole showing the anterior terminations of the cardinals. *n.*, notochord; *ao.*, aorta; *œs.*, cesophagus; *lg.*, lung; *v.p.c.r.*, *v.p.c.l.*, right and left posterior cardinals; *v.s.*, sinus venosus; *v.l.r.*, *v.l.l.*, right and left lateral veins; *v.v.*, vitelline vein; *pr.n.*, pronephros; *œl.*, coelom.

veins, which originally form a pair of small veins in the splanchnopleure along the sides of the yolk mass and liver-rudiment, have by this stage formed a system of sinus-like spaces, by spreading into and breaking up the anterior yolk mass into liver cylinders.¹ Tracing the common vitelline vein

¹ Shore, "Notes on the Origin of the Liver," *Journal of Anatomy and Physiology*, vol. v., N.S., 1891, p. 166.

backwards in the liver, it is found to separate into two tributaries, both of which are lost in the liver sinuses. One of these is well to the left side of the organ, and lies near the dorsal surface of the left lobe; the other is more definitely connected with the right lobe. Whether these tributaries are the original right and left vitelline veins I am unable to decide, the sections of intermediate specimens not being sufficiently clear on this point.

Returning to a 12-13 mm. tadpole, we find that the left tributary of the common vitelline vein is decidedly more pro-

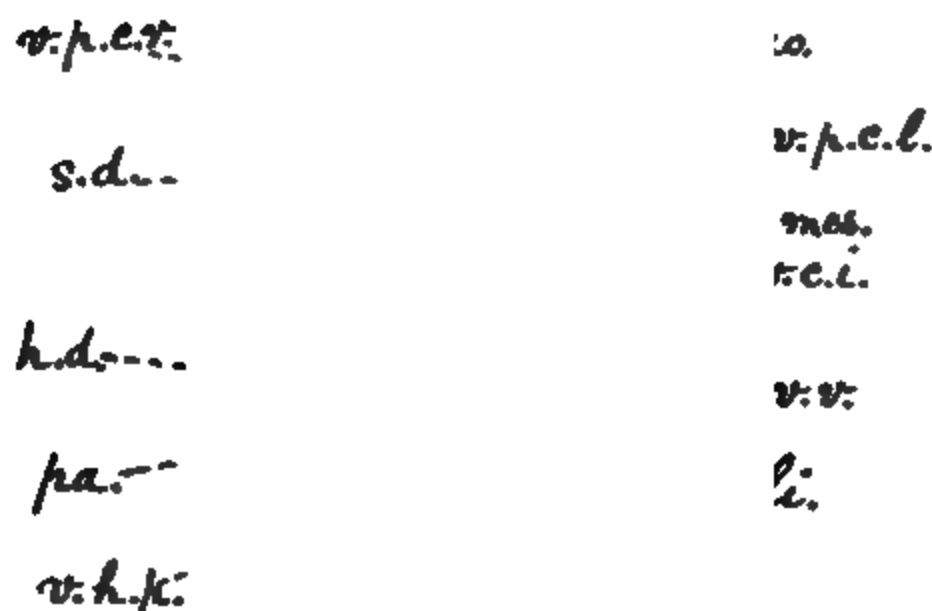


FIG. 7.—Transverse section of a 12 mm. tadpole showing the post-caval growing out from the vitelline vein to join the right posterior cardinal. *ao.*, aorta; *s.d.*, segmental duct; *mes.*, mesentery; *li.*, liver; *pa.*, pancreas; *h.d.*, hepatic duct; *v.h.p.*, hepatic portal vein; *v.v.*, vitelline vein; *v.p.c.r.*, *v.p.c.l.*, right and left posterior cardinal veins; *p.c.i.*, post-caval vein.

nounced than the other, but breaks up into the general vascular network of the organ. As we trace it through liver-substance, however, it again becomes more definite, approaches the dorsal part of the left side of the organ, and then, leaving the liver, can be followed through about five or six sections dorsalwards and backwards into direct continuity with the right posterior car-

dinal. This agrees with what Hochstetter¹ has described in *Lacerta*, except that he finds that the connecting vein grows out from the part of the vascular network of the liver formed by the *right* omphalomeseraic or vitelline vein, anastomoses having taken place between the right and left vitellines through the general hepatic vascular network. In figs. 7 and 8, drawings of two sections showing this connecting vessel are given. In fig. 7 it is shown just as it leaves the liver, and is seen to be lying in a fold of the dorsal mesentery. In fig. 8, which is drawn from the fourth section behind that of fig. 7, it is cut



FIG. 8.—Transverse section of a 12 mm. tadpole, the fourth section behind that of fig. 7, showing the junction of the post-caval with the right posterior cardinal. *aa.*, aorta; *s.d.*, segmental duct; *mes.*, mesentery; *h.d.*, hepatic duct; *li.*, liver; *v.h.p.*, hepatic portal vein; *v.c.i.*, post-caval vein; *v.p.c.r.*, *v.p.c.l.*, right and left posterior cardinal veins.

at its junction with the right cardinal. It is connected with the latter at the point, as described above, where the *oblique portion* of the cardinal begins. In a 12 mm. tadpole this connecting vessel is small, being less than half the size of the oblique part of the cardinal. It is, however, the beginning of what will ultimately form a considerable part of the length of

¹ Hochstetter, "Beiträge zur Entwicklungsgeschichte des Venensystems der Amnioten. II. Reptilien," *Morpholog. Jahrbuch.*, vol. xix., 1893, p. 428.

the post-caval. The accompanying diagram (fig. 9) will make the description clear.

Some care is required in examining the sections, for immediately posterior to the union of the vessel with the cardinal, the aorta, which here lies between and posterior to the cardinals, gives off its coeliaco-mesenteric branch, which passes ventrally and backwards in the mesentery toward the stomach, intestine, liver, and pancreas. When, as in a 12 mm. tadpole, the connection above described has been established, the blood, returning from the tail and right side of the body wall, can

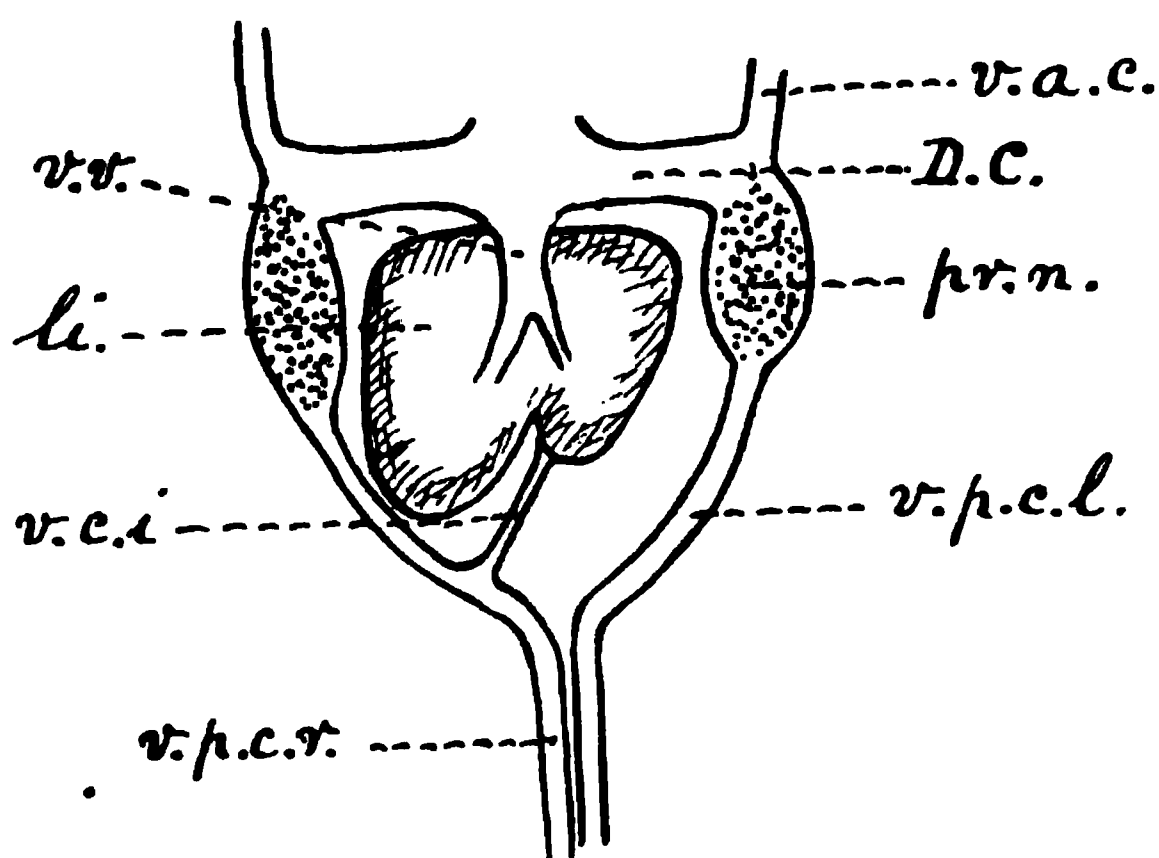


FIG. 9.—Diagram of the posterior cardinals of a 12 mm. tadpole. *D.C.*, Cuvierian duct; *li.*, liver; *pr.n.*, pronephros; *v.a.c.*, anterior cardinal vein; *v.c.i.*, rudiment of post-caval vein; *v.p.c.l.*, left posterior cardinal vein; *v.p.c.r.*, right posterior cardinal vein; *v.v.*, vitelline vein.

reach the heart either *via* the vascular network of the pronephros passing wholly in the posterior cardinal or *via* the mesonephric part of the cardinal, the incipient post-caval, the vascular network of the liver, and the common vitelline vein. At this stage the mesonephros is in quite an incipient condition, and the rudiments of the hinder limbs have only just begun to form; so that the post-caval can hardly be described as having been formed in the first instance in special relation to these organs, although, no doubt, it later forms the main venous connection between them and the heart. Exactly in what way the vascular connection between the right cardinal and the liver

becomes established I have been unable to determine, for I have not met with any intermediate conditions.

IV. *Union together of the Mesonephric parts of the Cardinals.*
—We have seen that in a 10 mm. tadpole the mesonephric parts of the cardinals lie side by side, ventral to the aorta from the bifurcation of the caudal vein to where they diverge into the oblique portions. The same is the case in a 12 mm. tadpole, the two vessels remaining separate for some time after the union of the post-caval with the right cardinal. In a 15 mm. tadpole, however, the two cardinals have begun to unite across the middle line ventrally to the aorta. They are separate in

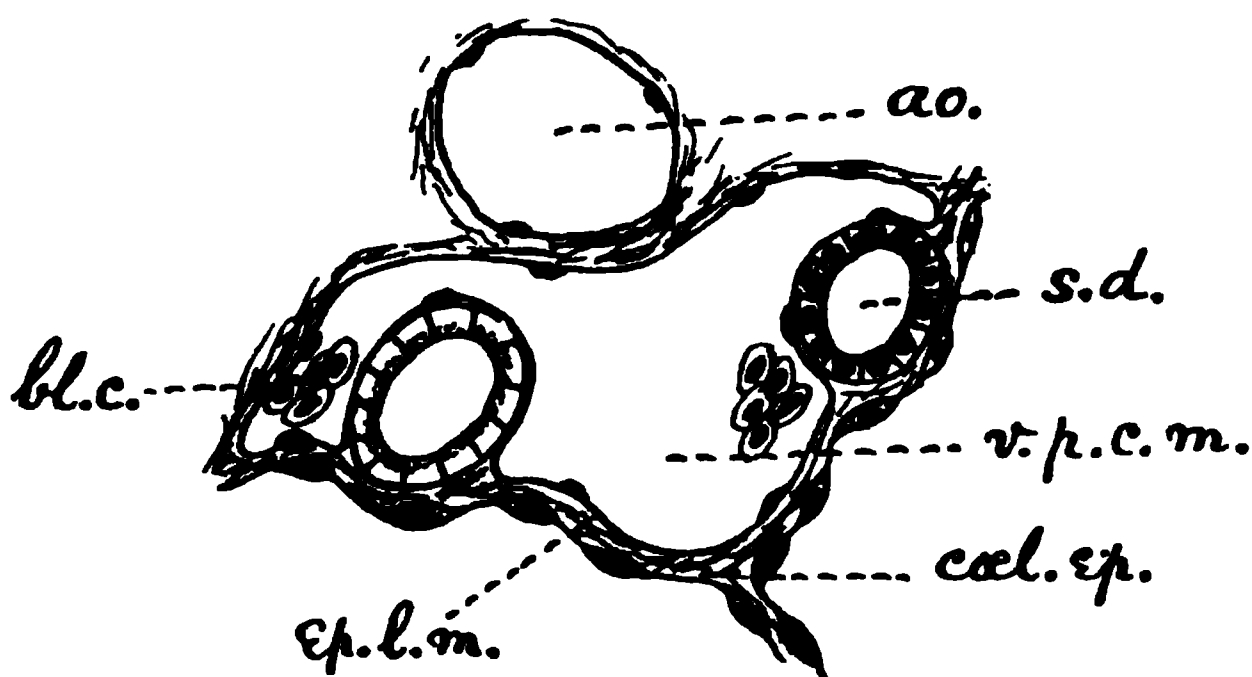


FIG. 10.—Transverse section of a 15 mm. tadpole through middle of mesonephric part of cardinals. *ao.*, aorta; *s.d.*, segmental duct; *bl.c.*, blood corpuscles; *coel.ep.*, coelomic epithelium; *ep.l.m.*, epithelial lining of sinus; *v.p.c.m.*, united posterior cardinals.

front of the origin of the coeliaco-mesenteric artery, but immediately behind this vessel, the left cardinal, which is now rather smaller than the right, has become united with the latter, and working backwards we find that they constitute a single median vessel through about three-quarters of the mesonephric part of their length. Posteriorly, the two cardinals are still separate, as in younger tadpoles. The relations of the united cardinals at this stage are shown in fig. 10. It will be seen that the greater part of the transverse diameter of the vein lies in the middle line between the segmental ducts and ventrally to the aorta, but a portion of the wall of the vessel is wrapped over the ducts, which have been, as it were, pushed into the vein. The thin epithelial lining of the vein can be

readily recognised by the small flattened nuclei, and is closely applied to the outer surfaces of the cells of the segmental ducts. In older tadpoles the union of the cardinals together becomes complete throughout the whole of their mesonephric parts, backwards to the caudal vein.

V. *Origin of the Mesonephros*.—The later history of the hinder part of the united cardinals is so intimately bound up with the development of the mesonephros that it is necessary to describe briefly the formation of this organ. The development of the excretory organs in Amphibia has been very fully elucidated by Götte¹ in Bombinator, by Fürbringer² in the Salamander, by Marshall and Bles³ in the Frog. It is necessary, therefore, to deal with the origin of the mesonephros only so far as concerns its relation to the cardinal vein. The first trace of the mesonephros is found in tadpoles of about 10 to 12 mm. It arises as a number of segmentally arranged masses of cells. They begin to be formed posteriorly near the termination of the segmental ducts in the cloaca. They are here for a time better marked and are further advanced in development posteriorly than anteriorly. Each cell-mass subsequently forms a nephridium. They arise in the mesoblast independently both of the coelomic epithelium and of the segmental duct. At first they are dorsal to the segmental duct and posterior cardinal vein. They consist of darkly staining masses of rounded cells with large nuclei, and their relations are well shown in fig. 11, which is a drawing of a section a short distance in front of the cloaca of a 12 mm. tadpole. The cell-masses are at first solid and rounded in form, but they subsequently grow into coiled cylinders, each of which becomes tubular and acquires a connection at one end with the segmental duct and at the other end a glomerulus forms. Subsequently nephrostomes are produced. The relations of the thin walls of the posterior cardinal veins to the cell-masses and segmental ducts shown in fig. 11 do not

¹ Götte, *Entwicklungsgeschichte d. Unke*, Leipzig, 1875.

² Fürbringer, *Zur Entwicklung d. Amphibienniere*, Heidelberg, 1877, and "Zur vergleichenden Anat. und Entwickl. der Excretionsorgane der Vertebraten," *Morphol. Jahrbuch.*, vol. iv., 1878.

³ Marshall and Bles, "The Development of the Kidneys and Fat Bodies in the Frog," *Studies from the Biol. Lab. of the Owens College*, vol. ii., 1890.

last long. In a 15 mm. tadpole the nephridial cylinders have begun to grow into the cardinal veins, which are beginning to be broken up into a network of venous sinuses closely surrounding the cylinders, similar to the condition around the pronephros. The flattened epithelial lining of the vein is traced as an accurately-fitting layer over the segmental duct and nephridia. This intimate connection of vein and mesonephros becomes a more striking feature as development proceeds. Meanwhile the whole cardinal vein (for the mesonephric parts of the two have by this time united into a median vessel) becomes greatly enlarged, *pari passu*, with the breaking up of



FIG. 11.—Transverse section of a 12 mm. tadpole to show the origin of the mesonephric nephridia. *neph.*, nephridium; *s.d.*, segmental duct; *coel.*, coelom; *coel.ep.*, coelomic epithelium.

its lumen into sinuses. This is well seen in an 18 mm. tadpole in which the union of the cardinals is complete back to the caudal. A drawing of a transverse section of an 18 mm. tadpole is shown in fig. 12. The great size of the united cardinals and the reflection of the vein-wall over the nephridia are obvious. The nuclei of the vein-wall contrast sharply with those of the nephridia and of the contained blood corpuscles. On both sides of the section the segmental ducts are completely enclosed by blood sinuses, and on the right side of the drawing (left of the tadpole) one nephrostome is shown. A careful examination of the series of sections fails to satisfy me that the nephrostome has any connection with a nephridium in the case of the particular one figured. I am inclined to think that the nephrostomes arise independently of the nephridia as invaginations of the coelomic epithelium, and not as Marshall described them, as outgrowths from the

nephridia near to the glomeruli which subsequently open into the coelom. With this point, however, we are not now concerned.

Although the united mesonephric parts of the cardinals become thus broken up into sinuses by the invasion of nephridia, yet the median part of it is a larger sinus than the rest, and in an 18 mm. tadpole forms what we may call the *median mesonephric channel*, into which smaller sinuses from the mesonephros open (see fig. 12, *v.c.i.*). The median mesonephric channel will subsequently form the hinder segment of the post-caval of the adult. Moreover, the lateral portions of the mesonephric



FIG. 12.—Transverse section of the posterior part of the mesonephros of an 18 mm. tadpole. *ao.*, aorta; *s.d.*, segmental duct; *neph.*, nephridia; *ep.l.m.*, epithelial lining of sinuses; *mes.*, mesentery; *n.st.*, nephrostome; *v.r.p.* (*mes.l.c.*), renal portal vein (lateral mesonephric channel); *v.c.i.* (*mes.m.c.*), post-caval vein (median mesonephric channel).

sinuses, which lie external to the segmental duct on each side, are more definite than the rest of the sinus, and can be traced through successive sections up the whole length of the mesonephros as a pair of *lateral mesonephric channels*. These will subsequently form the anterior portions of the renal-portal veins of the adult.

VI. *The Iliac Veins*.—The posterior limbs of the frog are formed as a pair of rounded buds from the somatopleure at the sides of the cloacal region, and are first recognisable in tadpoles of 12–13 mm. They consist of a dense mass of darkly-staining mesoblast, covered by a layer of cubical epiblast cells. The

buds grow slowly, but shortly after their formation a pair of iliac veins may be recognised. They are connected in front with the cardinals near the bifurcation of the caudal, and, tracing them backwards, we find them as a pair of small vessels alongside the caudal vein, through a few sections only, gradually diverging and becoming smaller as they pass outwards towards the rudiments of the limbs. Here they are lost. Later on, during the growth of the mesonephroi and their encroachment on the median cardinal, the iliacs can be traced *from the sides* of the enlarged united cardinals, and the caudal is the continuation of the cardinal in the middle line. A section from an

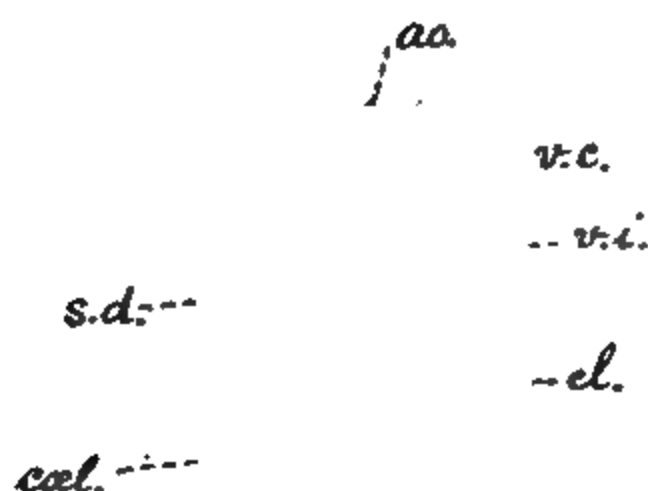


FIG. 13.—Transverse section of an 18 mm. tadpole through junction of segmental ducts and cloaca. *ao.*, aorta; *s.d.*, segmental duct; *cl.*, cloaca; *coel.*, coelom; *v.c.*, caudal vein; *v.i.*, iliac vein.

18 mm. tadpole is figured in fig. 13. This section is taken at the level of the termination of the segmental ducts, behind the mesonephros, and is from the same tadpole as the section drawn in fig. 12. It shows the median caudal vein (*v.c.*) and the iliacs (*v.i.*), lying just external to their corresponding segmental ducts. If the series of sections be traced backwards from that of fig. 12 to that of fig. 13, we find that the cardinal sinus surrounding the nephridial tubules maintains a large size as far back as the most posterior nephridium, where the vessel almost suddenly narrows and passes into the three veins shown in fig. 13. The median mesonephric channel, which, as already stated, becomes the hinder segment of the adult post-caval, is

continuous with the caudal, and the lateral mesonephric channels, which become the anterior portions of the renal-portals of the adult, directly join the iliacs.

VII. *Degeneration of the Pronephros*.—The pronephros and the large cardinal sinus which surrounds it on each side are at their highest development in tadpoles from 15–18 mm.; and during the period when the tadpole grows from 9 or 10 mm. to 18 mm. in length, it forms the main excretory organ. When, however, the mesonephros has attained the condition found in tadpoles of from 18–20 mm. (*i.e.*, possesses tubular nephridia which have joined the segmental duct, and has become surrounded by the blood sinuses of the median cardinal), the pronephros begins to degenerate. Commencing degeneration of it can first be made out in tadpoles of about 18 mm., and progresses steadily throughout the remainder of tadpole life, till at the time of metamorphosis only a small remnant of these once important organs is found in the shape of a few pigmented remains of tubules. The nature of the degeneration changes and their effects on the posterior cardinals can be well studied in tadpoles of 23, 25, and 30 mm. in length. Some of the tubules of the pronephros become dilated, others compressed, and the vein-sinuses between them obviously obstructed. The part of the segmental duct between the pronephros and the mesonephros becomes first small, afterwards obstructed, and finally entirely lost. Probably the narrowing and obstruction of it is to a large extent the cause of the degeneration of the pronephric nephridia. In a 25 mm. tadpole, whilst the mesonephric part of the cardinals is the enormously dilated structure already described, the oblique portions of the cardinals are now quite small vessels, and the sinuses of the pronephros have nothing like their former development. As to the pronephric nephridia themselves, the cells become flattened, their inner surfaces indefinite, frayed out and granular, and the lumina of the tubules become more or less filled with granules of epithelial debris, or with cells and nuclei in a state of partial disintegration.

Meanwhile the post-caval vein, whose connection with the right cardinal in a 12 mm. tadpole has been described, has

become greatly enlarged, and is now more obviously the functional proximal continuation of the mesonephric parts of the cardinals. In fact, the post-caval, as in the adult, now constitutes the chief vein of the posterior part of the trunk. Starting from the caudal vein it is traced as the median mesonephric channel, between the mesonephroi, then from the anterior end of these it passes in a fold of mesentery to the dorsal surface of the liver, giving off laterally the still traceable oblique parts of the cardinals. On the dorsal side of the liver it now receives the hepatic veins, and is continued directly into the sinus venosus of the heart.

VIII. *Formation of the Renal-portal Veins.*—We have already traced the formation, from the cardinals, of the lateral mesonephric channels, and have learnt that when the iliac veins arise, they become continuous with these lateral mesonephric channels, *i.e.*, with the posterior cardinals. We have now to deal with the further history of these veins after the stage of the 18 mm. tadpole, as figured in figs. 12 and 13. In tadpoles of 25–30 mm. the disposition of these venous channels has not altered much, but on tracing the iliac veins from the mesonephroi to the corresponding limbs, we find that they are obviously formed of two tributaries, which unite at the root of the limb-bud, from which point they are traced distally as separate vessels, to be lost in the limb-buds. One tributary passes rather to the dorsal side of the limb-rudiment, and the other more definitely to its ventral side. These I identify as the sciatic and femoral veins of the adult. The ventral or femoral tributary receives several small veins from the cloaca and posterior part of the abdominal wall. These occupy a position very like that of the pelvic veins at the time of metamorphosis, and although I have not been able quite to settle the point, I incline to think that one or more of these small veins becomes dilated to form the pelvics. If so, it is interesting to note that, in the first instance, the pelvics carry blood from the abdominal walls *into* the iliacs and not the reverse. Sections of tadpoles in the later stages of larval life show clearly that the iliacs give rise to the greater part of the length of the adult renal-portals, whilst the anterior parts of the renal-portals

where they lie along the outer borders of the mesonephroi are formed from the lateral mesonephric channels. In fig. 14 I give a diagram to show these points. A is a diagram of the venous arrangement in a 25-30 mm. tadpole, and B shows the vessels of the adult, and how they have been formed.

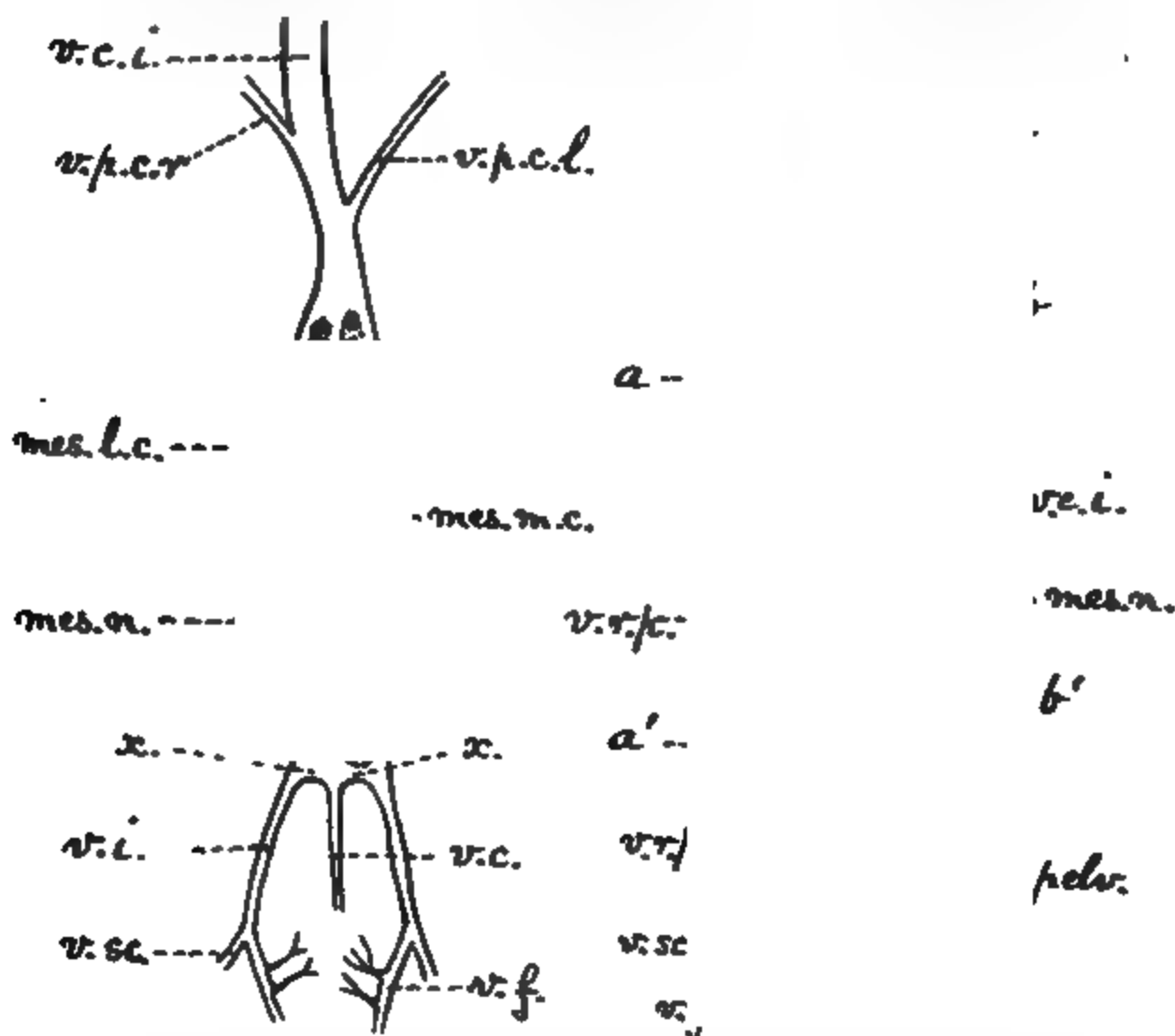


FIG. 14. — Diagrams of the venous arrangements. A, in a 25-30 mm. tadpole. B, in the adult. *a, a'*, part of the renal-portal formed from the cardinal; *b, b'*, part of the post-caval formed from the cardinal; *mes.n.*, mesonephros; *mes.m.c.*, median mesonephric channel; *mes.l.c.*, lateral mesonephric channel; *v.c.*, caudal vein; *v.c.i.*, post-caval vein; *v.f.*, femoral vein; *v.i.*, iliac vein; *v.p.c.l.*, left posterior cardinal; *v.p.c.r.*, right cardinal; *v.r.p.*, renal-portal vein; *v.sc.*, sciatic vein; *v.pelv.*, pelvic vein; *x*, connecting channel between the caudal and lateral mesonephric channel.

In fig. 14 B, the caudal vein, and the oblique and pronephric parts of the cardinals which disappear are dotted; the part of the renal-portal, between the lines lettered *a, a'*, is formed from the cardinal, and the portion of the post-caval produced from the cardinals lies between the lines lettered *b, b'*.

IX. *Fate of the Posterior Cardinals.*—We have already traced the changes in the cardinals up to the establishment of the mesonephroi, and have followed how their united mesonephric portions have in an 18 mm. tadpole become split up into (a) a median mesonephric channel, (b) the venous sinuses around the mesonephric nephridia, and (c) the lateral mesonephric channels. These three parts are, of course, in full communication with each other. We have seen how the median mesonephric channel forms a part of the post-caval, and the lateral channels parts of the renal-portals of the adult. It only remains now to trace the fate of the rest of the cardinals. In regard to the pronephric part of each cardinal, we have already seen that it has begun to dwindle in a 23–25 mm. tadpole; from that stage onwards, during the rest of larval life, it becomes less and less distinct, until by the time of metamorphosis, the whole of each cardinal in front of the point of junction of the post-caval had practically disappeared. The caudal continuation of the median mesonephric channel likewise disappears with the loss of the tail. The remaining portions, viz., those which form the vascular sinuses in the substance of the mesonephros ultimately form the capillary system (except glomeruli) within the adult organ connecting the renal-portals and the renal veins. The mouths of opening of these sinuses into the median mesonephric channel form the renal veins (mesonephric) of the adult.

X. *General and Historical.*—The account given in the foregoing pages will be seen to afford a complete and obvious explanation of the two abnormal specimens of the renal-portal system, described in this *Journal*, vol. xiv., N.S., p. 398, and vol. xv., N.S., p. 323. Several further points of interest arise from the consideration of the facts above detailed.

1. In the *first* place, the earliest arrangement which I have described of the caudal and posterior cardinals, before the establishment of any renal-portal system in the 10 mm. tadpole, reminds one very much of the plan found in the adult *Petromyzon*, in which the cardinals arise by a bifurcation of the caudal and run forwards, receiving vessels from the mesonephroi but without forming any renal-portal system.

2. *Secondly*, it should be noted that the term “renal-portal

vein," or *vena renalis advehens*, has been rather loosely applied to what would appear to be morphologically different structures. (a) In Elasmobranch fishes, the renal-portals are formed by a bifurcation of the caudal, receive the small iliac veins from the pelvic fins, and pass to the outer and ventral aspect of the corresponding kidney (metanephros), the cardinals arising from renal veins along the inner sides of these organs.

(b) In *Rana*, on the other hand, the renal-portal of the adult has no connection with the caudal, but is formed of the iliac. In the early frog-tadpole, however, there is a condition resembling that of the Elasmobranch fishes. The parts of the mesonephric sinus, marked x in fig. 14 A, by which the caudal is connected with the lateral mesonephric channels, seem to me to be equivalent to the roots from the caudal of the renal-portals of the Elasmobranchs. It seems to me that the arrangement in the adult frog is a secondary one, derived from a more primitive type of renal-portal system, like that of Elasmobranchs.

(c) In this connection it is interesting to compare the renal portal system of the Salamander with that of the frog on the one hand and of the Elasmobranch on the other. In the Salamander the renal-portals arise from bifurcation of the caudal as in the Elasmobranch, but along the outer border of the kidney (mesonephros) each receives a branch from the iliac, the rest of which passes on as a pelvic vein to form an anterior abdominal as in the frog. The arrangement of the post-caval and anterior parts of the cardinals is in Salamander strikingly similar to that of a 25-30 mm. frog-tadpole. The renal veins form a median post-caval between the kidneys; then in front of the kidneys the post-caval gives off a pair of azygos cardinal veins which run forwards to join the subclavians, and the right one arises from the post-caval a little anterior to the other, showing probably that in development the primitive post-caval from the liver joined with the right cardinal as in the frog. Hochstetter's¹ account of the development of these veins in *Salamandra atra* confirms this, for he found that the caudal bifurcates into posterior cardinals, and that the posterior parts of the latter become divided into an outer and inner trunk reuniting in front.

¹ Hochstetter, "Beiträge z. Anat. und Entwick. des Venensystems der Amphib. u. Fische," *Morph. Jahrbuch.*, vol. xii., 1888, p. 119.

The primitive post-caval joins the right cardinal, and the two inner portions of their hinder sections unite together to form the mesonephric part of the cava, whilst the outer divisions of the hinder parts of the cardinals form the renal-portals.

(d) Although in Salamander the renal-portals are like those of Elasmobranchs rather than of *Rana*, we find in *Ceratodus* an arrangement more like that of the frog. In *Ceratodus* the caudal vein bifurcates between the kidneys (mesonephroi) into, on the left side, the posterior cardinal, and on the right the larger post-caval vein, *without forming a renal-portal system*. The renal portals of *Ceratodus* are formed by the iliacs, each of which bifurcates into a dorsal renal-portal and a ventral pelvic to form an anterior abdominal as in the frog. The co-existence in *Ceratodus* of a left posterior cardinal with a post-caval vein on the right side is interesting. It would appear that the primitive post-caval is formed as in the frog, and joins the *right* posterior cardinal, the hinder part of which, *without joining the left cardinal*, becomes converted into the hinder part of the caval.

(e) In *Lacerta* the renal-portal system combines the features of Elasmobranchs and of the frog. The caudal vein divides into right and left renal-portals, which, before they reach the kidneys (metanephroi), are joined by a branch from the iliacs, formed by the confluence of femorals and sciatics, the rest of the iliacs passing on to join into an anterior abdominal. Moreover, in the arrangement of its post-caval, *Lacerta* is more primitive than *Rana*. The renal veins form on each side a longitudinal vessel, of which the right is larger than the left, and is directly continued into the post-caval, whilst the left at the level of the gonads crosses the middle line to join the cava. I regard these longitudinal vessels from their point of junction backwards as parts of the original cardinals, and it would seem that the primitive caval had joined the *right* cardinal as in the frog, but that the two cardinals had remained separate posteriorly except at the point of junction above referred to. It must, however, be pointed out that this interpretation of the condition in *Lacerta* does not agree with Rathke's account of the development of the vena renalis advehens and post-caval in the snake.¹ Rathke states that the hinder parts of the posterior cardinals persist

¹ Rathke, *Entwicklungs. d. Natter*, 1839.

along the outer borders of the kidneys as the *venæ renales advehentes*, and that the post-caval does not unite behind with the cardinals. Balfour,¹ from his observations on *Lacerta*, was inclined to accept Rathke's account. Götte,² on the other hand, in his famous memoir, described the relations of the post-caval of *Amphibia* to the posterior cardinals. His account is directly opposed to Rathke's and Balfour's observations on *Reptilia*, but my observations on the vena cava of the frog completely confirm Götte's, though my results on the origin of the renal-portals do not quite agree with his. More recently, Hochstetter³ has worked out the development of these veins in *Lacerta agilis*. His results agree with Rathke's, but as they differ considerably from my own observations in the frog, we must briefly refer to them. Hochstetter finds that at an early stage the caudal bifurcates into a pair of vessels passing along the *inner* borders of the kidneys and ending in these organs, thus having the relations of "renal-portal veins." Along the *outer* borders of the kidneys there are formed a pair of veins which receive vessels *from* the kidneys and somatic veins along their course, and are continuous in front with the posterior cardinals, which have a sinus-like character in connection with the anterior part of the kidney (? pronephros), and posteriorly are continuous with the iliacs. At this stage the cardinals act as *venæ renales revehentes*. Subsequently, the primitive cava is formed, and becomes continuous behind, with *both* of the vessels lying on the *inner* sides of the kidneys, which become united together for some distance. The blood from the caudal can now return direct to the heart without going through a renal-portal system, and the vessels lying on the inner borders of the kidneys now become *venæ renales revehentes*, and the direction of flow of blood through the kidney *becomes reversed*, the iliacs and cardinals on the *outer* borders of the kidneys becoming *venæ renales advehentes*. Anastomoses between the iliacs and caudal are subsequently formed, and apparently the posterior parts of the two original branches of the caudal disappear, their anterior parts forming the two radicles of the post-caval of the adult.

¹ Balfour, *Comparative Embryology*, vol. ii., 1881, p. 540, footnote.

² Götte, *Entwicklungsgeschichte d. Unke*, Leipzig, 1874.

³ Hochstetter, "Beiträge zur Entwicklungsgeschichte des Venensystems der Amnioten. II. Reptilien," *Morph. Jahrbuch.*, vol. xix., 1893, p. 428.

The remarkable points in this history are:—(a) that in the early embryo the *primary* venæ renales advehentes are branches of the caudal, as in Elasmobranchs; (β) that they are then independent of the iliacs, which pass straight into the cardinals; (γ) that later on, with the establishment of the post-caval (which does not join the cardinals but the *primary* venæ renales advehentes), *the circulation through the kidney is reversed, the anterior parts of the primary venæ renales advehentes becoming venæ renales revehentes in the adult, and the posterior section of the cardinals becoming the adult venæ renales advehentes.* A careful study of Hochstetter's memoir and of his drawings leads me to think that he has overlooked an earlier stage before the formation of the kidneys, and that the two branches of the caudal (*primary* venæ advehentes) and the "posterior cardinals" on the outer sides of the kidneys, with the vascular capillary system of the kidneys themselves, are really all parts of an original pair of posterior cardinals, connected behind with the caudal, substantially like those of a 10 mm. tadpole. If this conclusion should ultimately turn out to be correct, then the main outlines of the development of the renal-portals and fate of the cardinals in the Lizard would substantially agree with my results for the frog.

3. *Thirdly*, the sinus-like character of the pronephric and mesonephric parts of the cardinals, and the intimate relation of the lining of flattened epithelial cells to the nephridial tubules deserves attention. This close connection of the veins with the pronephros was described by Götte¹ and by Marshall² in Bombinator and Frog, as well as by Fürbringer³ in Salamander. It has also been referred to by Felix⁴ in Teleosteans, and by Minot⁵ in the pronephros of Teleosteans and Ganoids, and tailed Amphibians. Minot also pointed out the sinus-like character of the vessels of the mesonephros of the pig and of the adult frog. He drew attention to the sharp distinc-

¹ Götte, *loc. cit.*

² Marshall, *Vertebrate Embryology*.

³ Fürbringer, *loc. cit.*

⁴ Felix, "Beiträge z. Entwick. der Salmoniden," *Anatomische Hefte*, vol. viii., 1897, p. 251.

⁵ Minot, "On the Veins of the Wolffian bodies in the Pig," *Proc. of the Boston Society of Natural History*, vol. x., 1898, p. 265.

tion between the mesonephros and metanephros of Amniota generally. In the metanephros the inter-tubular vessels are true capillaries, and not sinuses. He makes the interesting suggestion that, if this difference should prove to be general as between the pro- and meso-nephros on the one hand, and the metanephros on the other, it may establish a morphological difference between the two sets of organs, and show that the metanephros is not phylogenetically related to nephridia, but is a new formation (*l.c.*, page 272).

The same sinus-like character of the vascular network of the adult vertebrate liver was pointed out by Lewis Jones and myself, for we found in no case any basement membrane between the liver cells and the blood channels, and in several instances, *e.g.*, eel, frog, newt, tortoise, chick, etc., we found that the blood spaces have the same sinus-like character as in the mesonephros of the frog, and that the flattened epithelial walls of the sinuses are closely "adapted to the irregular surfaces of the tubules around them."¹

In a subsequent paper,² I figured the same feature in the embryonic liver of the chick and cat. There is, however, this difference between the sinus-like system of the mesonephros and that of the liver. The former is the result of the penetration of the nephridia into the cardinal vein, whilst in the liver "there take place irruptions, as it were, of capillary blood-vessels from the vitelline vein into the solid mass of proliferated hypoblast."³

The striking resemblance in these vascular relations between the pronephros, mesonephros, and the liver, has, I am sure, some important morphological and physiological meaning.

XI. *Conclusions.*—From my observations, as described in the foregoing account, the following conclusions are established:—

A. *As to the fate of the posterior cardinal veins in the frog.*

1. The anterior portions of both cardinals, from the point of junction of the primitive cava with the right cardinal forwards

¹ Shore and Jones, "On the structure of the Vertebrate Liver," *Journal of Physiology*, vol. x., 1889, p. 408. (See plate xxviii., figs. 7 and 8.)

² Shore, "Notes on the Origin of the Liver," *Journal of Anatomy and Physiology*, vol. v., N.S., page 166.

³ *Loc. cit.*, page 184.

through the pronephroi to their termination in the Cuvierian vein, disappear.

2. The posterior parts of the cardinals, from the point of junction of the cava with the right cardinal backwards, first of all unite into a median vessel. This median vessel gives rise to—

- (a) The posterior section of the adult post-caval, *i.e.*, that part of it which lies between the mesonephroi.
- (b) The mesonephric or renal veins.
- (c) The sinus-like vascular network within the substance of the kidney, and connecting the renal-portal veins with the mesonephric veins.
- (d) The anterior portions of the adult renal-portal veins, *i.e.*, the parts which lie along the outer borders of the mesonephroi.

3. The caudal continuation of the cardinals disappear.

B. *As to the origin of the renal-portals.*

1. There are two types of renal-portal systems—(a) like that of Elasmobranch fishes, in which the renal-portals begin from a bifurcation of the caudal vein. This is found in an early frog-tadpole, and may be called the *primary renal-portal system*. Probably in this type the renal-portals are developed from the posterior cardinals, the kidneys being interposed between an anterior and a posterior section; (b) like that of the adult frog, in which the renal-portals have no connection with the caudal, but arise mainly from the iliacs. This type may be called the *secondary renal-portal system*.

2. The anterior parts of the renal portals of the adult frog (secondary renal-portal system) are formed from the lateral parts of the united hinder ends of the cardinals (lateral mesonephric channels).

3. The posterior portions of the renal-portals, *i.e.*, from the bifurcation of the femorals into renal-portals and pelvis forwards to the hinder ends of the mesonephroi are formed from the iliac veins.

Incidentally in this research, which was primarily undertaken to determine the development of the renal-portals, questions have arisen as to—

1. The formation of the post-caval vein. How much of it is formed from the original vitelline vein, and exactly how the connection between the liver veins and the posterior cardinal is established.

2. The development of the pelvic veins and their connection with the iliacs.

3. The mode of formation of the anterior abdominal and how it acquires its connection with the liver.

On these points I have already a good deal of material, and shall hope to deal with them shortly.

"SOCIA THYMI CERVICALIS," AND THYMUS ACCESSORIUS.¹ By N. BISHOP HARMAN, M.A., M.R. (Cantab.), F.R.C.S. (Eng.) (*From the Cambridge University Anatomical Schools.*)

THE subjects in which these forms of thymus glands were found were full-timed fetuses.

1. "SOCIA THYMI CERVICALIS."

In the thymus gland possessing the associated part to which I have applied this name, on the analogy of the Socia parotidis, there is an extension, or rather a retention, of gland tissue along the track of origin of the main gland. It is shown in fig. 1.

In the undissected condition the thoracic thymus appeared as an undivided mass from which there were two unequal prolongations upward into the neck; these were asymmetrical, the right side showing a short conical process, whilst the left side possessed a much larger prolongation, which was continued as a long tortuous fleshy process of varying size, to reach a level slightly above the upper border of the ala of the thyroid cartilage and under cover of the angle of the mandible.

The base of this prolongation or socia was continuous with the main thoracic thymus in the same manner as the short conical process of the right side; at the root of the neck its size was reduced until it became a narrow flexuous cord of a slightly firmer consistency than the normal thymus tissue. At the level of the isthmus thyroideæ it enlarged considerably, and exhibited an irregularly-shaped fleshy mass, having a typical thymic glandular appearance, in shape, in marks of lobulation, and in consistency. It terminated in a large lobule, which was doubled upon itself; and connected with the mass of the socia by a short narrow neck. Throughout its course it

¹ Read at the meeting of the British Medical Association, 1901.

possessed the pinkish colour characteristic of the thoracic thymus.

It was situated laterally to the trachea and laryngeal carti-

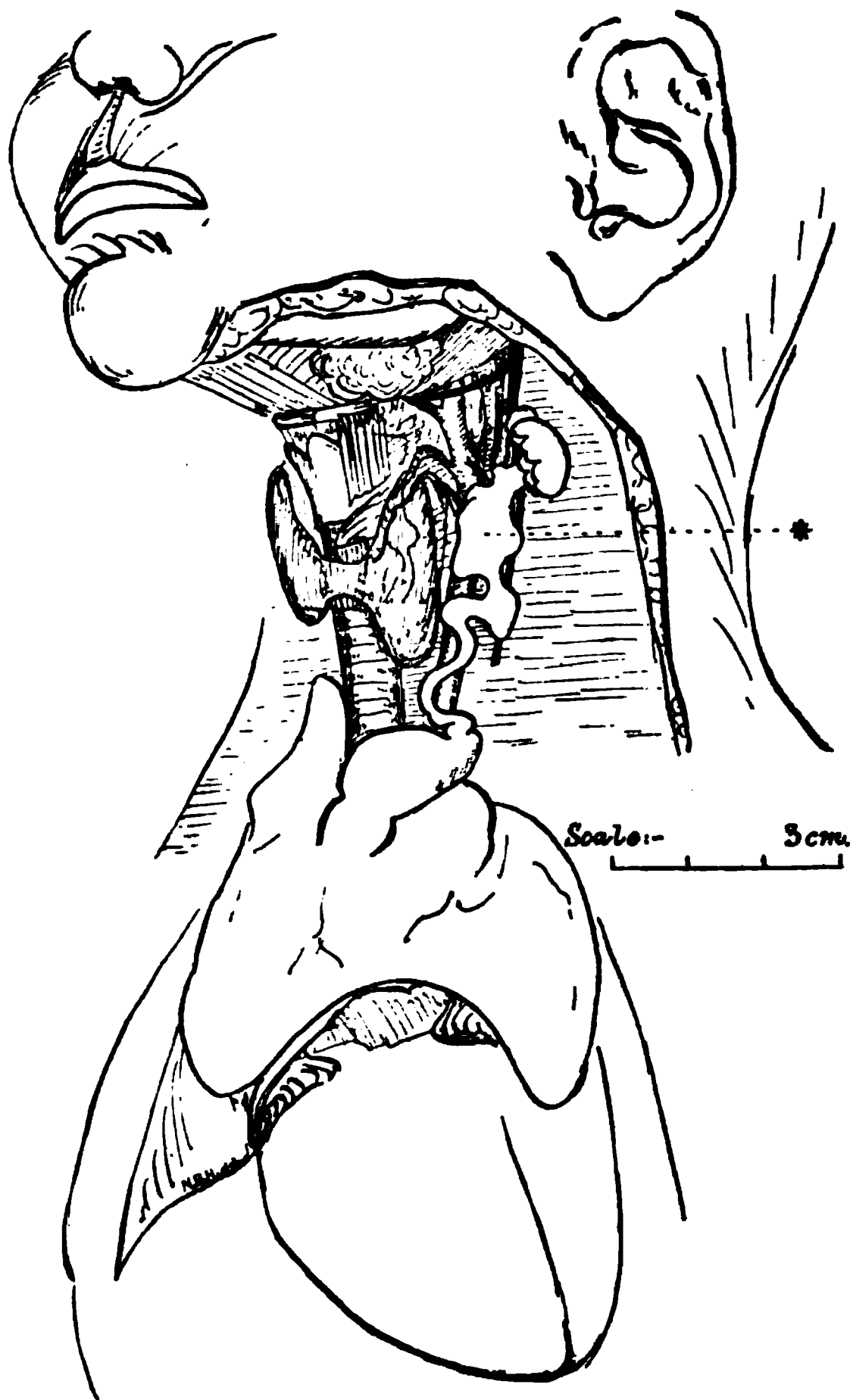


FIG. 1.—The body was placed dorso-decubitus, with the head twisted sharply to the right. * Indicates the socia.

lages, having the internal jugular vein over its superficial aspect, and the common external and internal carotid arteries, with the vagus nerve, as deep relations. During its tortuous course it was at various times internal, superficial, and external to the

vessels. The relation of the vagus nerve to its upper part was peculiar; the highest lobule was, as stated above, connected with the mass of the socia by a narrow neck; this neck was encircled by two divisions of the vagus nerve, which formed an annulus. From the anterior division the N. descendens cervicis arose, and after crossing the socia superficially, descended to reach its muscular distribution.¹

A definite vascular supply was found for the socia, viz.:—Arterial: by a small branch springing directly from the external carotid slightly distal to its origin, and also by twigs from the common carotid and superior thyroid arteries. Venous: a fair-sized branch issued to join the superior thyroid vein.

A careful dissection was made to ascertain any possible connection the socia might have with the pharynx or with the thyroid gland, but none was found.

Removal of the connective tissue capsule of the whole thymus showed that the connection of the socia with the main mass was by continuous thymus tissue, leading into a central lobe of considerable size; this central lobe was in its turn connected with the more lateral lobes by blood-vessels and loose areolar tissue only.

The capsule of the socia was removable with an ease characteristic of the thymus, and widely different from the more tenacious covering of the thyroid.

A portion of the highest lobule was removed for microscopical examination. It shows characters typical of the thymus gland—Lymphoid tissue in masses, with the concentric corpuscles of Hassall.

Such a condition of the gland as this has, I believe, not been previously noticed in man.

Astley Cooper (1, plate iii., fig. 5), writes (page 4):—"In many subjects I have examined, the cervical portion of the thymus passes higher upon the right than upon the left side, and I have generally seen it joined by a ligament to the larynx, and by vessels to the thyroid gland." The prolongation here described is on the left side, and far exceeds in length the process described by Cooper.

¹ This tertiary origin of the N. descendens cervicis by way of the vagus nerve I have met with more frequently in the dissection of fœtuses than in that of adults.

2. THYMUS ACCESSORIUS.

This form is represented in fig. 2; it was found in a male foetus 53 cm. long.

A small oval body of about $9 \times 9 \times 7$ mm. lay immediately ventral and to the leftward of the trachea, in juxtaposition to the lower edge of the left lateral lobe of the thyroid gland and the upper limit of the corresponding lobe of the thymus gland.

It was pink in colour, of a paler shade than that of the

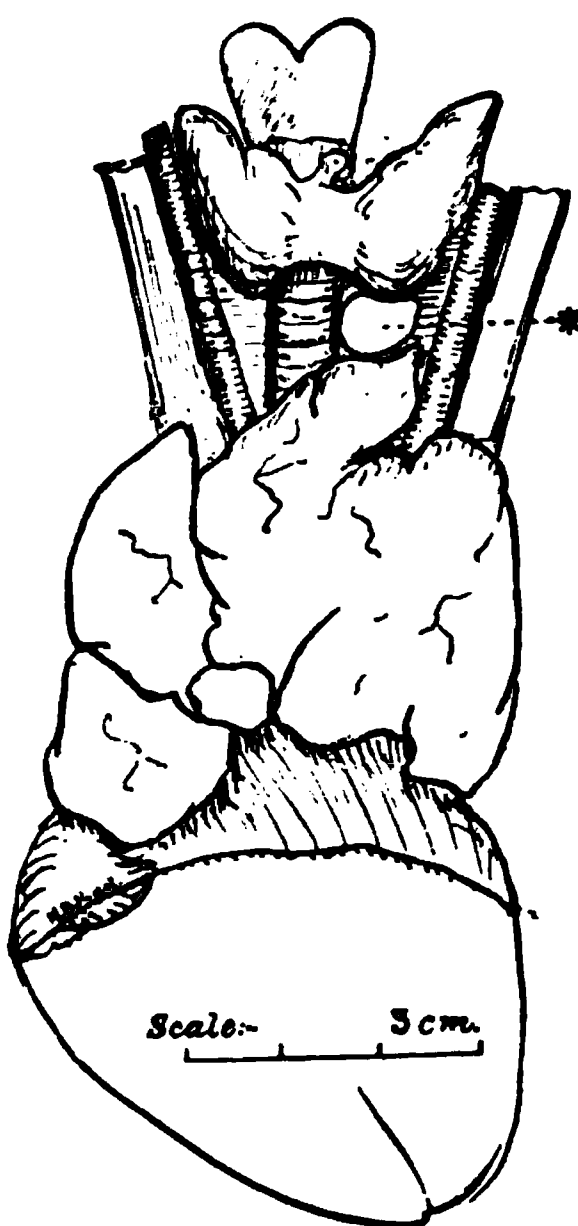


FIG. 2.

thymus mass, and totally different from the rich purple of the thyroid gland.

Removal of the environing connective tissue showed that it had no connection of any kind with the thymus gland, whereas it was firmly fixed to the trachea and lower border of the thyroid gland; to the latter it was also connected by its vascular supply, the inferior thyroid artery and vein.

A portion of the accessory gland was removed for micro-

scopical examination; this also exhibited characters typical of the thymus—lymphoid tissue in masses, with the concentric corpuscles of Hassall.

The position of this body was similar to that usually occupied by the inferior parathyroid body, but it was definitely characteristic of a thymic body; still, by way of comparison, the parathyroid glands, including the left inferior, were dissected out in a recently deceased adult, and sections prepared therefrom, when the distinction was complete.

3. THE SIGNIFICANCE OF THESE VARIATIONS.

(a) *Of the Socia thymi cervicalis.*

The greatest interest of the socia lies in its likeness to the form of thymus usual for birds, reptiles and some young mammals. In birds it extends as a narrow strip beside the long trachea from larynx to bronchi. In lambs I have noticed it extends so high in the neck as to be severed by the slaughterer's knife on transfixion of the neck.

Astley Cooper (1), describing the thymus of the calf, writes: "It reaches from the anterior mediastinum above the pericardium, to the angle of the lower jaw, extending by its cornua on each side of the neck, and at the angle of the inferior maxillary bone it doubles upon itself, so that its length is somewhat increased." This description, save that it is for bilateral cornua, exactly tallies with the condition found in this case, even to the doubling of the final portion.

The descriptions and figures of Simon (7, page 41, figs. 12, 13 and 14), for the Lemur, *Pteropus edulis*, and *Galeopithecus* are singularly like the arrangement in this specimen, save that in all these cases the arrangement is bilateral. Simon says of the lemur: "A slender prolongation reaches upwards on each side the trachea and expands in the vicinity of the larynx." He also comments upon the slenderness of the union of the thoracic and cervical portions of the gland in the sloth.

Embryologists agree in placing the origin of this gland from the region of gill pouch III, the situation of which was immediately anterior to the thyroid cartilage. This socia extended to a level equal with this site; so, from its histological character, its likeness as regards position to the common form found in

lower animals, and from our knowledge of its source in man (His), there can be no doubt that this socia with a part of the main mass of the thymus represents a retention of the whole of the lateral outgrowth of gill pouch III, which normally goes to form the thymus gland.

It seems that an interesting significance may be attached to the relation of the vagus nerve to the neck of the socia. In examining several sections of embryos of *Mustelus laevis*, it was noticed that as the lateral branches of the vagus nerve left the main trunk, they passed over the dorsal prolongations of the gill pouches which represent the anlagen of the thymus: it seems likely that the anterior part of the annulus of the vagus which encircled the socia may represent such a lateral branch, which has rejoined the main trunk to proceed to its destination, which has been rendered posterior by the growth of the neck. Unfortunately the vagus had been purposely cut at the root of the neck in an earlier dissection, so that this point could not be worked out.

(b) *Of the Thymus Accessorius.*

An accessory thymus has been described frequently. Henle figures one in his text-book (3). This, he says, is distinctly isolated from the main mass of the gland. Jendrassik (5) states that such an accessory body may be found even 'on or in' the thyroid gland. Kohn (6) describes two small masses of 'adenoid' tissue closely united to each lateral lobe of the thyroid gland; and Welsh (8) speaks of thymus residues occurring as nodules of thymus tissue on the posterior surface of the lateral thyroid bodies.

The presence of such an accessory thymus may, I think, be found to bear a more important interpretation than residues.

His (4), in his investigations on human embryology, places the origin of this gland from the gill pouch III only. Upon this evidence alone it would be difficult to account for the presence of such definitely isolated or accessory masses.

De Meuron (2), in his thesis on the development of the organ, shows that in passing from a lower to a higher organism there can be found a concurrent decrease in the extent of the site over which the gland arises; so that whilst in the skate all five

gill slits are functional in the origin of the gland (Dohrn), for the shark the origin is from clefts II, III, IV, and V; in the mammal (sheep) the origin is restricted to slits III and IV, and in this case the main mass is derived from one cleft only, the third. He figures (plate xxvii. fig. 3) a semi-schematic arrangement for the sheep, in which two large longitudinal lobes are shown as derived from pouches III, whilst two small round thymic bodies are shown situated immediately posterior to the lower border of the lateral thyroid lobes; these he states are derived from gill pouches IV. The situation of these bodies in the sheep is identical with the position in which was found the accessory thymus described above. It seems, therefore, that a comparison of De Meuron's observation on the sheep, with the occurrence of these isolated masses in man, will tend to show that whilst His' statement as to the origin of the gland from a single gill pouch may be the general rule for man, and De Meuron's view of a progressive diminution of the extent of the origin of the gland with an ascent in the animal scale is supported by such a finding, yet there may be in some cases an extra origin of the gland from the fourth gill pouch in man, which will be found to persist as an accessory thymus such as represented here.

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tion between the mesonephros and metanephros of Amniota generally. In the metanephros the inter-tubular vessels are true capillaries, and not sinuses. He makes the interesting suggestion that, if this difference should prove to be general as between the pro- and meso-nephros on the one hand, and the metanephros on the other, it may establish a morphological difference between the two sets of organs, and show that the metanephros is not phylogenetically related to nephridia, but is a new formation (*l.c.*, page 272).

The same sinus-like character of the vascular network of the adult vertebrate liver was pointed out by Lewis Jones and myself, for we found in no case any basement membrane between the liver cells and the blood channels, and in several instances, *e.g.*, eel, frog, newt, tortoise, chick, etc., we found that the blood spaces have the same sinus-like character as in the mesonephros of the frog, and that the flattened epithelial walls of the sinuses are closely "adapted to the irregular surfaces of the tubules around them."¹

In a subsequent paper,² I figured the same feature in the embryonic liver of the chick and cat. There is, however, this difference between the sinus-like system of the mesonephros and that of the liver. The former is the result of the penetration of the nephridia into the cardinal vein, whilst in the liver "there take place irruptions, as it were, of capillary blood-vessels from the vitelline vein into the solid mass of proliferated hypoblast."³

The striking resemblance in these vascular relations between the pronephros, mesonephros, and the liver, has, I am sure, some important morphological and physiological meaning.

XI. *Conclusions.*—From my observations, as described in the foregoing account, the following conclusions are established:—

A. *As to the fate of the posterior cardinal veins in the frog.*

1. The anterior portions of both cardinals, from the point of junction of the primitive cava with the right cardinal forwards

¹ Shore and Jones, "On the structure of the Vertebrate Liver," *Journal of Physiology*, vol. x., 1889, p. 408. (See plate xxviii., figs. 7 and 8.)

² Shore, "Notes on the Origin of the Liver," *Journal of Anatomy and Physiology*, vol. v., N.S., page 166.

³ *Loc. cit.*, page 184.

through the pronephroi to their termination in the Cuvierian vein, disappear.

2. The posterior parts of the cardinals, from the point of junction of the cava with the right cardinal backwards, first of all unite into a median vessel. This median vessel gives rise to—

- (a) The posterior section of the adult post-caval, *i.e.*, that part of it which lies between the mesonephroi.
- (b) The mesonephric or renal veins.
- (c) The sinus-like vascular network within the substance of the kidney, and connecting the renal-portal veins with the mesonephric veins.
- (d) The anterior portions of the adult renal-portal veins, *i.e.*, the parts which lie along the outer borders of the mesonephroi.

3. The caudal continuation of the cardinals disappear.

B. *As to the origin of the renal-portals.*

1. There are two types of renal-portal systems—(a) like that of Elasmobranch fishes, in which the renal-portals begin from a bifurcation of the caudal vein. This is found in an early frog-tadpole, and may be called the *primary renal-portal system*. Probably in this type the renal-portals are developed from the posterior cardinals, the kidneys being interposed between an anterior and a posterior section; (b) like that of the adult frog, in which the renal-portals have no connection with the caudal, but arise mainly from the iliacs. This type may be called the *secondary renal-portal system*.

2. The anterior parts of the renal portals of the adult frog (secondary renal-portal system) are formed from the lateral parts of the united hinder ends of the cardinals (lateral mesonephric channels).

3. The posterior portions of the renal-portals, *i.e.*, from the bifurcation of the femorals into renal-portals and pelvis forwards to the hinder ends of the mesonephroi are formed from the iliac veins.

Incidentally in this research, which was primarily undertaken to determine the development of the renal-portals, questions have arisen as to—

ordinary dimensions. A triangular flattened piece of bone,

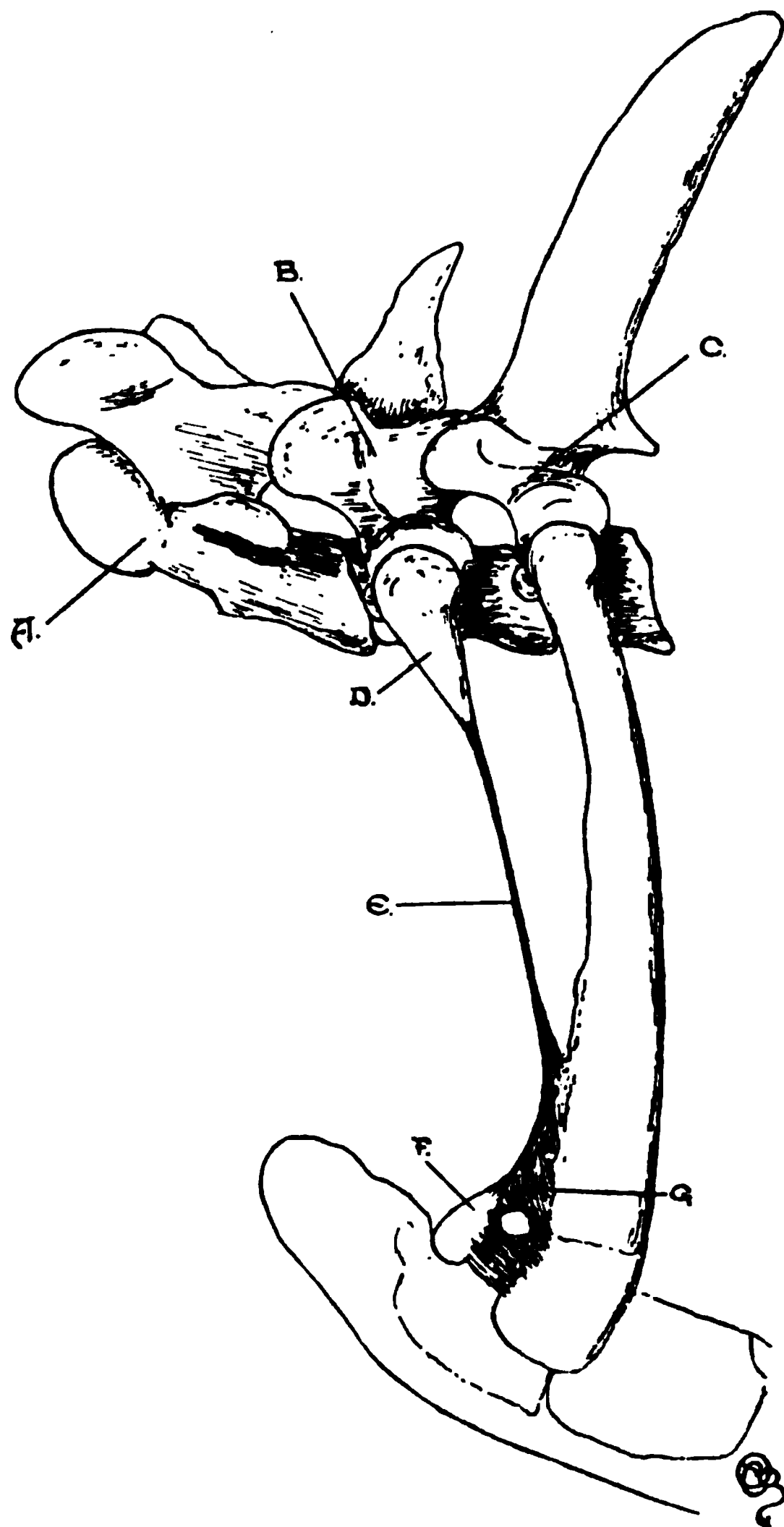


FIG. 1.—A=seventh cervical vertebra ; B=first thoracic vertebra ; C=second thoracic vertebra ; D=rudimentary first thoracic rib ; E=fibrous cord continuing rudimentary rib ; F=nodule of bone representing sternal end of rudimentary rib ; G=fibrous tissue filling in ventral part of first interspace.

attached by fibrous tissue to the sternum, doubtless represented

the sternal end of each rib (fig. 1, F). The intervening segment of the rib was replaced by a strong, rounded fibrous cord of about 4 mm. in thickness (fig. 1, E). This was firmly attached to a rough and slightly projecting surface close to the junction of the middle and ventral thirds of the cephalic border of the 2nd rib. Excepting that its ventral part was somewhat broader than usual, the second rib presented no noteworthy features.

As a consequence of the attachment of the fibrous continuation of the 1st to the border of the 2nd rib, the first intercostal space was divided into two unequal parts, the dorsal of which was

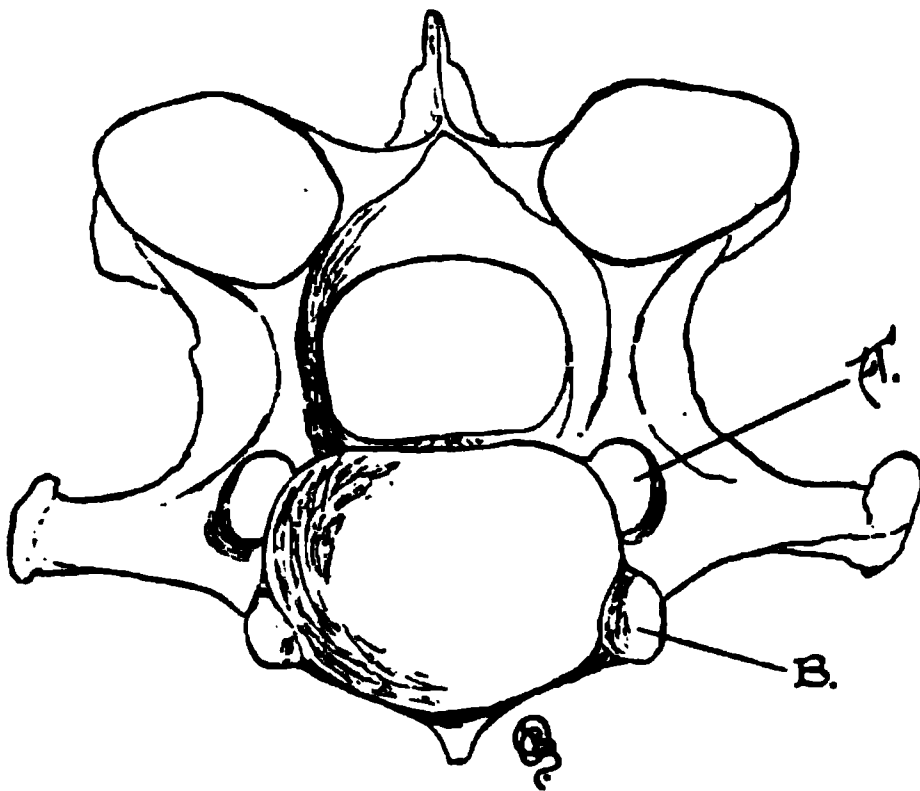


FIG. 2.—Seventh cervical vertebra.

A = vertebrarterial foramen.

B = concavity for articulation with the head of the first rib.

occupied by intercostal muscles in the ordinary way. The ventral, and smaller, portion of the interspace was filled in by a strong sheet of fibrous tissue in which was an opening for the passage of a large perforating branch of the internal mammary artery (fig. 1, G).

In correspondence to the reduced size of the head of the first rib, the concavity formed by the bodies of the 7th cervical and 1st thoracic vertebræ was much smaller than usual. The 7th cervical vertebra presented a remarkable feature inasmuch as there was a vertebrarterial foramen piercing the root of each of its transverse processes (fig. 2).

The scaleni muscles, failing to find a sufficiently ample area

for attachment on the rudimentary rib and its fibrous continuation, were largely inserted into the cephalic border of the 2nd rib. For a similar reason the pectoral prolongation of the rectus abdominis was attached to the 2nd rib instead of the 1st.

The vertebral artery passed through the vertebrarterial foramen of the 7th vertebra.

Otherwise than in the above particulars, the disposition of the structures in the neighbourhood of the entrance to the thorax followed the text-book descriptions with a remarkable degree of closeness.

Bearing in mind the circumstance that the development of cervical ribs is, from phylogenetic reasons, of more frequent occurrence than the imperfect development of the 1st thoracic rib, and remembering, moreover, that some observers are of opinion that many, if not most, of the variations usually placed in the latter category should by rights be regarded as belonging to the former, the question which first suggested itself was whether this case might not be one in which cervical ribs were present. There seems little doubt that this question may be answered in the negative. The vertebrae were present in the usual number, and, apart from the possession of vertebrarterial foramina by the 7th, their form did not present any peculiarities. There could be no doubt that the vertebra to which the rudimentary rib belonged was the 1st thoracic. Further, the brachial plexus was examined with care and was found to be constituted, in the usual way, by the 6th, 7th, 8th, 9th, and 10th spinal nerves; these nerves sharing in its formation in the customary proportions. Taking all the facts into account, there can be little doubt that it was the first pair of thoracic ribs which had failed to attain to their normal degree of development.

Although the occurrence of cases in which the 1st thoracic rib—if we accept Rosenberg's views—is undergoing a change of a progressive nature is generally held to be rare, a study of the literature leads one to conclude that, in all probability, the rarity has been over-estimated.

Helm (8) collected sixteen cases recorded between the years 1853 and 1885; but it is very probable that his list is not

complete. This supposition is originated by his omission of several cases of so-called bicipital ribs mentioned in a paper by Turner (9), who considers them to be the result of fusion of the 1st and 2nd thoracic ribs; cases which should, without doubt, be included in the list.

Since the appearance of Helm's paper several communications have been published in which rudimentary 1st ribs have been described. Hertslet and Keith (10) have put on record a case in which the condition was present on both sides of the body, and Low (11) one with a unilateral deficiency. Leboucq (5) has discussed at some length three occurrences of the abnormality, two of which are of rudimentary 1st ribs as generally recognised, while the third is of a rib divided into vertebral and sternal portions 25 mm. from the lateral border of the sternum, an articulation occurring between the two segments. A parallel to this last form of variation is found in a record by Heusinger (12).

The most recent addition to the literature is made by Dwight (7) in a paper on the human spines showing numerical variation in the Warren Museum of the Harvard Medical School. Forty-five complete spines are passed under review, among which are two cases of rudimentary 1st thoracic rib, both unilateral. In addition to these forty-five complete spines, some thirteen incomplete specimens are mentioned, from which two examples of rudimentary 1st rib are obtained, and one of fusion of the 1st and 2nd ribs.

Dwight's paper, valuable for many reasons, is useful in that it affords a means by which the relative frequency of cervical and rudimentary 1st thoracic ribs may be computed. No previous writer has given such full data. In the forty-five complete specimens cervical ribs occur seven times, whereas rudimentary thoracic ribs are only present twice. Among the thirteen disjointed fragments there are two instances of each of these deviations from the normal, and one example of fusion of the 1st and 2nd ribs. The much rarer character of a defect in the 1st rib is strikingly illustrated.

All the papers mentioned above deal with human spines. The literature is not nearly so rich in instances in the lower animals, possibly because the defect is less common in them.

than in man, but very probably because so much attention has not been paid to variations in the skeleton of members of the animal kingdom other than *Homo*.

I have only been able to find records of two cases that were not human. Struthers (13), in a foot-note to his very valuable paper on vertebral and costal variations, states that, in the skeleton of a three-toed sloth (*Bradypus tridactylus*) the 1st thoracic rib "on the right side begins by head and tubercle attachments, but its shaft is only half an inch in length and terminates, in the macerated bone, by an irregular blunt end."

Hermann Adolphi (14) describes a case in a dog in which the 1st rib was defectively developed on both sides of the body. On the right side the head and tubercle were normal, but the body was slender and short, and did not reach the sternum. There was no evidence of a costal cartilage. On the left there was neither head nor neck, but the body was of more perfect development than on the right side, and a costal cartilage was present. Considerable interest attaches itself to this case because of an attempt at the formation of a rib on the right side of the 21st vertebra; the same side of the body, it will be noted, as that on which the 1st rib was the more rudimentary.

The case in the horse, which is the subject of the present paper, is worthy of record for several reasons. Not the least important of these is the fact that the vertebræ were normal in number, and, with the exception of the 7th cervical, also in form. The 7th vertebra had the ordinary general form, but was unusual in that the transverse processes were provided with foramina. This is a condition which, though varying much in different mammals, is very rarely found in the horse. An examination of all the equine 7th vertebræ in the osteological collection of this College fails to unearth any specimen in which there is even an attempt at the production of a foramen. Struthers (13) notes that there is a horse's skeleton in the Anatomical Museum of the University of Aberdeen in which "the foramen is present on the right side and is fully as large and as rounded as that of the 6th vertebra, and bounded below by as thick a bony wall, fully

ankylosed." In my case the foramen is present on both sides, and is large and well formed; but the transverse processes do not otherwise differ from the normal either in size, shape, or direction; whereas in Struthers' case the process beyond the foramen "is thickly bifurcated; the superior part prolonged backwards; the inferior projecting forwards, and also continued backwards on the body of the vertebra."

The degree of development, or rather of defect of development, does not appear to be greater than has been found in many of the cases already recorded. It appears, further, that it is not unusual for that part of the rib which has failed to ossify to be represented by a fibrous cord. And there is apparently a great tendency for this cord to establish a connection with the 2nd rib. Indeed it seems to be almost a law that a rudimentary 1st rib seeks to become blended with its more perfect next-door neighbour, this being most evident in those fusions which result in so-called bicipital ribs.

The presence of a nodule of bone attached to the sternum is also not uncommon, and is of great interest as showing that it is the middle part of the body of the rib that becomes defective, the dorsal and ventral ends remaining more or less perfect. A fact of some importance in this connection has been observed by Leboucq (6). He points out that the 1st rib has apparently a tendency to divide into two segments—a vertebral and a sternal—and that it is at the level of this division that the rib first inclines to become rudimentary. Moreover, in cases where cervical ribs are present, a sternal nodule is sometimes found. And, again, it is admitted that the manubrium normally contains the sternal ends of ribs.

The altered attachment of muscles in these cases gives an indication of how a muscle may be lengthened or shortened because of its having to seek a new and sufficiently firm foothold when its usual origin or insertion is no longer physiologically possible.

In conclusion, it may perhaps be permissible to emphasise the fact that, in the case I have described, the condition was symmetrical; a feature not usual, but of some phylogenetic importance.

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**A CASE OF CONGENITAL MALFORMATION OF THE
HEART, WITH ABNORMALITIES OF ABDOMINAL
VISCERA: ABSENCE OF SPLEEN, ABSENCE OF
HEPATIC SECTION OF INFERIOR CAVA. By
T. W. P. LAWRENCE, F.R.C.S., and DAVID NABARRO, M.D.**

THE patient, a female child, aged 14 weeks, was admitted into the Evelina Hospital for Children, Southwark, under the care of Dr Nestor Tirard, through whose courtesy we are enabled to publish a record of the case.

The history of the patient is briefly as follows:—The child was of a “mottled blue” colour at birth, and when she coughed or cried, the cyanosis was more marked, especially about the face and head. The extremities, too, were very blue at times. The mother states that the child’s breathing was “very short and quick,” and that she “struggled at times to get her breath.” When she cried, the cry was always weak and “stifled.” When five or six weeks old the child suffered from an attack of diarrhoea and vomiting, and from that time the cyanosis was more marked as well as more permanent. She was admitted to hospital on 8th June 1901, when she was very blue, the temperature never reached 97° F., the pulse rate was 128–144 per minute, and the respirations 72 to 100 per minute.

We did not see the child during life, and there was some doubt as to the presence of a cardiac murmur.

The child died on June 10th, having been in the hospital only two days; there were no fits, and death seems to have been due to respiratory failure.

The child’s parents are both healthy; they have had four other children, three of whom are alive and well, the fourth having died of “bronchitis and convulsions.”

Owing to some delay in obtaining the necessary sanction, the post-mortem examination was not done until about 40 hours after death. Weight of child, 7½ lbs. On opening the body in the usual way, the heart was found in its normal position with

its apex well over to the left, but considerably increased in size, so that only a thin anterior border of the right lung was visible, while of the left lung only a trace was visible at the top of the thorax. From the front no interventricular furrow was discernible, suggesting that only a single ventricle was present. The veins on the anterior surface of the heart were prominent and distended, indicating that the child had died in an asphyxial condition. The pulmonary artery lay in front of the



FIG. 1.—General view of the Viscera on opening the thorax and abdomen.

R.L., right lung; L.L., left lung; P.A., pulmonary artery; Ht., heart; L., liver; G.B., gall-bladder; St., stomach; L.I., large intestine; S.I., small intestine.

aorta and rather more to the left than normal; it was large (diam. 15 mm.), and gave off two branches to the lungs as usual. The aorta arose behind and rather to the right of the pulmonary trunk, so that in the undissected state it was practically hidden by the pulmonary artery. In diameter the aorta was considerably smaller than the pulmonary trunk (diam. of aorta 10 mm.). The three primary trunks given off from the aortic arch and

their chief branches were normal. After giving off the left subclavian artery, the aorta narrowed down considerably (diam. 4 mm.), and after a course of 6 mm. in this narrowed condition was joined by a patent ductus arteriosus, the descending aorta being formed by the fusion of the two. The ductus arteriosus was 4 mm. long and rather under 4 mm. in diameter; its wall was considerably thicker than that of the isthmus aortæ, indicating probably that obliteration of the lumen was beginning to take place.

The rest of the aorta was normal in its position and branches.

The right coronary artery, arising from the aorta at a spot between the pulmonary artery and the right auricular appendix, passed to the right in the auriculo-ventricular groove, giving off infundibular and marginal branches in the normal way. It terminated on the hinder surface of the heart as a very slender vessel which turned downwards into the posterior interven-tricular groove.

The left coronary artery, arising from the aorta between the pulmonary artery and the left auricular appendix, divided almost immediately into two branches, one of which entered the substance of the right ventricle, while the other passed to the right side in the auriculo-ventricular groove, and gave off a slender descending branch which coursed downwards on the hinder aspect of the heart in the interventricular sulcus, corresponding to the anterior interventricular groove of the normal organ.

On examining the right auricle, the caval apertures were found in the usual positions, but the superior vena cava seemed larger than normal. The cavity of the auricle was considerably enlarged, and the wall somewhat thickened. The interauricular septum was well formed, but the foramen ovale was patent, being an oval slit 5 mm. long. There was a large well-formed auricular appendix. The right auriculo-ventricular orifice was distinctly enlarged; the valve had the usual three flaps, the edges of which were, however, definitely thickened and irregular. On opening the right ventricle, the wall of this chamber was seen to be greatly thickened, and the cavity much dilated. The infundibulum was distinct and the pulmonary artery arose from its upper and left part. The pulmonary valve had three flaps,

and on one a definite fibrous nodule was present. Immediately below and behind the orifice of the pulmonary artery was a thick muscular ridge, in the position of the free inferior border of the aortic septum, while immediately posterior to this muscular ridge was the orifice of the aorta communicating directly with the right ventricle. The aortic valve had three flaps, which appeared to be slightly thickened. The long axis of the right ventricle measured about 5.8 cm., and the right ventricle alone formed the apex of the heart.

Only three pulmonary veins entered the left auricle, and on opening up this chamber its cavity was seen to be very much smaller than that of the right auricle (about a quarter or a third the size). The wall was very much thickened. In the floor of the left auricle there was a small depression, but no left auriculo-ventricular orifice was present. There was a small but well-developed auricular appendix. When the heart was first examined, although the right ventricle had been opened in two different places, no trace of a left ventricle was seen, and it appeared as if the heart had only one ventricle from which arose the aorta and pulmonary artery. When examined more closely, however, in the posterior wall of the right ventricle there was a narrow, cleft-like space, which on being opened out was seen to have a smooth lining of endocardium, and to be provided with rudimentary columnæ carneæ. This cavity is that of the left ventricle greatly reduced in size; and in all probability during life it was merely a potential cavity, the interventricular septum being closely applied to the peripheral wall of the left ventricle. Had the cut in the heart not been made exactly where it was, it seems quite possible that one would have overlooked the remnant of a left ventricle (especially as no auriculo-ventricular orifice was present) and described the heart as consisting of one ventricle only, which functionally was the case.

From the upper extremity of this slit-like cavity a probe passed over the upper edge of the fleshy interventricular septum into the aorta. The probe was then seen from the cavity of the right ventricle through the interventricular foramen. There was no indication of valve flaps corresponding to a left auriculo-ventricular orifice. The long axis of the left ventricle measured

2.8 cm., and a probe 4 mm. thick could pass through the aperture at the upper extremity. The muscular septum of the ventricles (septum inferius) extended upwards to within 7 mm. of the thick muscular ridge representing the free edge of the aortic septum, the interval between the two being the interventricular foramen (fig. 2 B).

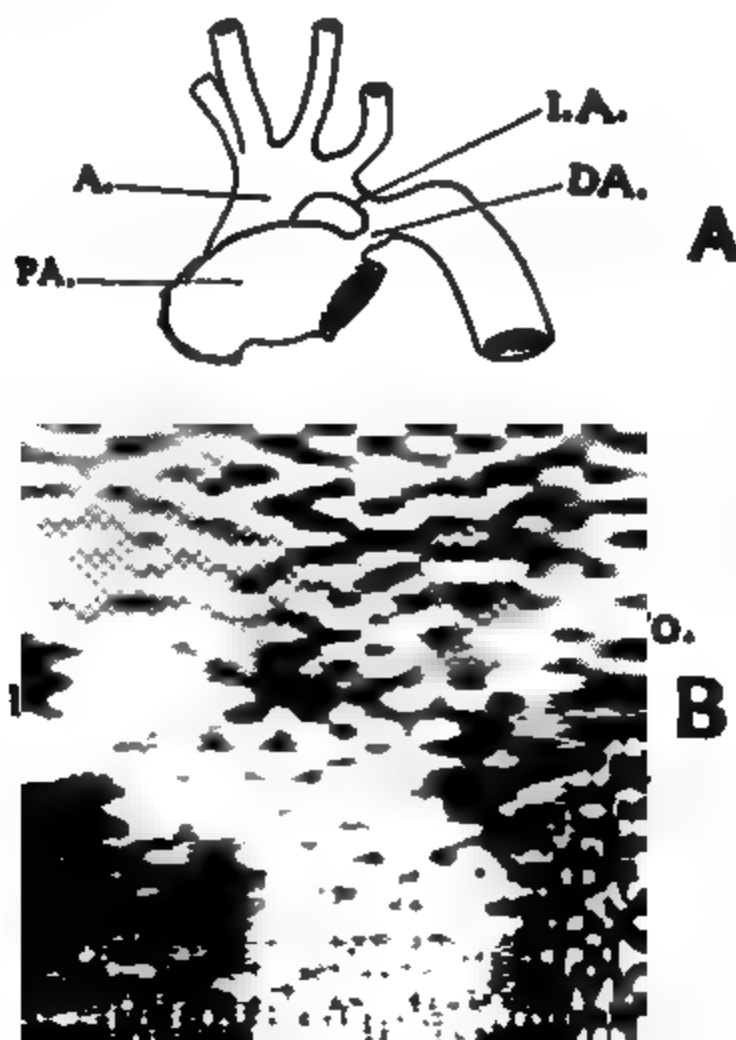


FIG. 2, A.—View of pulmonary artery, arch of aorta with its branches and the ductus arteriosus.

B.—Semi diagrammatic section of heart showing slit-like left ventricle, absence of left auriculo-ventricular orifice, thickened extremity of aortic septum, and the interventricular foramen.

A., aorta; A.S., muscular ridge corresponding in position to lower border of aortic septum; A.V.O., depression in position of the left auriculo-ventricular opening; D.A., ductus arteriosus; I.F., interventricular foramen; L.A., left auricle; L.V., left ventricle; P.A., pulmonary artery; R.A., right auricle; R.V., right ventricle; S.I., septum inferius; I.A., isthmus aortæ.

The wall of the left ventricle was considerably thinner than that of the right, but when the interventricular septum was applied to the wall of the left ventricle, as was the case when the heart was first cut into, the resulting apparently simple

wall of the ventricle was rather thicker on that side than on the right side of the heart.

The heart was very considerably enlarged, its weight (with a couple of inches of the main arteries attached) being 63 grammes or nearly three times the weight of the heart in a child of about 7 lbs.

In the right lung, the middle lobe was not marked off and the pulmonary artery passed above the main bronchus, which gave off no eparterial bronchus. On the left side the arrangement was normal, two lobes only being present. On section the lungs seemed healthy, there was no sign of consolidation or atelectasis. The right lung weighed 78 grms. (2·75 ozs.), the left 62 grms. (2·25 ozs.).

The Thymus was very small (2·8 grms.), the atrophy being possibly due to the pressure of the enlarged heart.

The Abdominal Organs.—On reflecting the abdominal walls the liver was seen to be in its normal position, but the stomach, instead of lying behind the left lobe, came down from under the right lobe of the liver. The pyloric end was in the median plane and anterior to the cardiac end, which was more deeply placed than, and to the right of, the pylorus. The small omentum stretched across from the small curvature of the stomach to the liver, and formed a covering to the abnormal prolongation of the liver, shortly to be described. The stomach did not extend to the left beyond the middle line, but the duodenum lay entirely to the left of the spine on the left kidney, the first and second parts curving round the pancreas. The small intestines lay completely in the left half of the abdomen. The large intestine was in the hypogastric and right and left iliac regions, and the part seen on opening the abdomen, without disturbing the viscera, nowhere rose higher than the lower third of the abdominal cavity.

The cæcum was situated in the middle line, just behind the left border of the stomach, and the appendix was directed upwards so as almost to touch the under surface of the liver. The “ascending colon,” passing to the right from the cæcum, was entirely concealed by the stomach and was twisted on itself in the form of a volvulus, an “ascending mesocolon” being present. The “transverse” and “descending” colon were

represented by several coils in the lowest part of the abdomen, and seemed to pass directly into the rectum, the bowel being completely covered with peritoneum and provided with a mesentery until the rectum was reached. There was a marked constriction in the large bowel about 10 inches beyond the cæcum, the peritoneal covering at this spot having fibrous bands in it, which, by their contraction, had possibly given rise to the narrowing.

The intestines were otherwise healthy—no sign of a Meckel's diverticulum being present. The pancreas was small and folded on itself, showing no separation into head and tail. It lay in the middle line over the spine and was surrounded by the duodenum on two sides. Its weight was 4·2 grms. The kidneys and suprarenal capsules were normal in situation and apparently healthy. Each kidney weighed 21·7 grms., and each suprarenal capsule 1·9 grms.

No trace of a spleen could be found, nor on careful examination was any representative or spleniculus discoverable in the great omentum or elsewhere. Mr Walker Edmunds, F.R.C.S., Surgeon to the Evelina Hospital, and Mr J. B. Addison, the R.M.O., were present at the autopsy and joined in the search for the spleen. The kidneys, suprarenal capsules and all the abdominal organs were removed from the body, and the pelvis was also searched for the spleen, but in vain.

The mesenteric glands were slightly enlarged, but not more so than is generally found in children who have suffered from diarrhoea and vomiting before death. They were flesh-coloured and not dark purplish, like a spleen.

The general form of the liver was normal, but on the under surface of the left lobe there was a tongue-like process measuring 3 cm. ($1\frac{1}{4}$ ins.) in length and 18 mm. ($\frac{3}{4}$ in.) in breadth, which arose close to, and to the left of, the posterior part of the longitudinal fissure. The spigelian and caudate lobes were not marked off, and there was no trace of a vena cava inferior. The round ligament of the liver was bridged over by a well-developed "pons hepatis" and joined the portal vein.

The portal vein itself divided into two main branches, the right branch immediately giving off two large branches to the right lobe while the left gave off a small branch to the abnormal process

mentioned above, and then supplied the left lobe. Attached to the main trunk of the portal vein posteriorly was a slender fibrous cord which narrowed very rapidly and was apparently attached to one of the hepatic veins. It was, however, quite impervious, and not even a depression was visible at its attachment to the portal vein. From the upper part of the posterior border of the liver four hepatic veins emerged, two from each lobe of the liver, but the common trunk of the hepatic vein was unfortunately not preserved with the specimen. The small

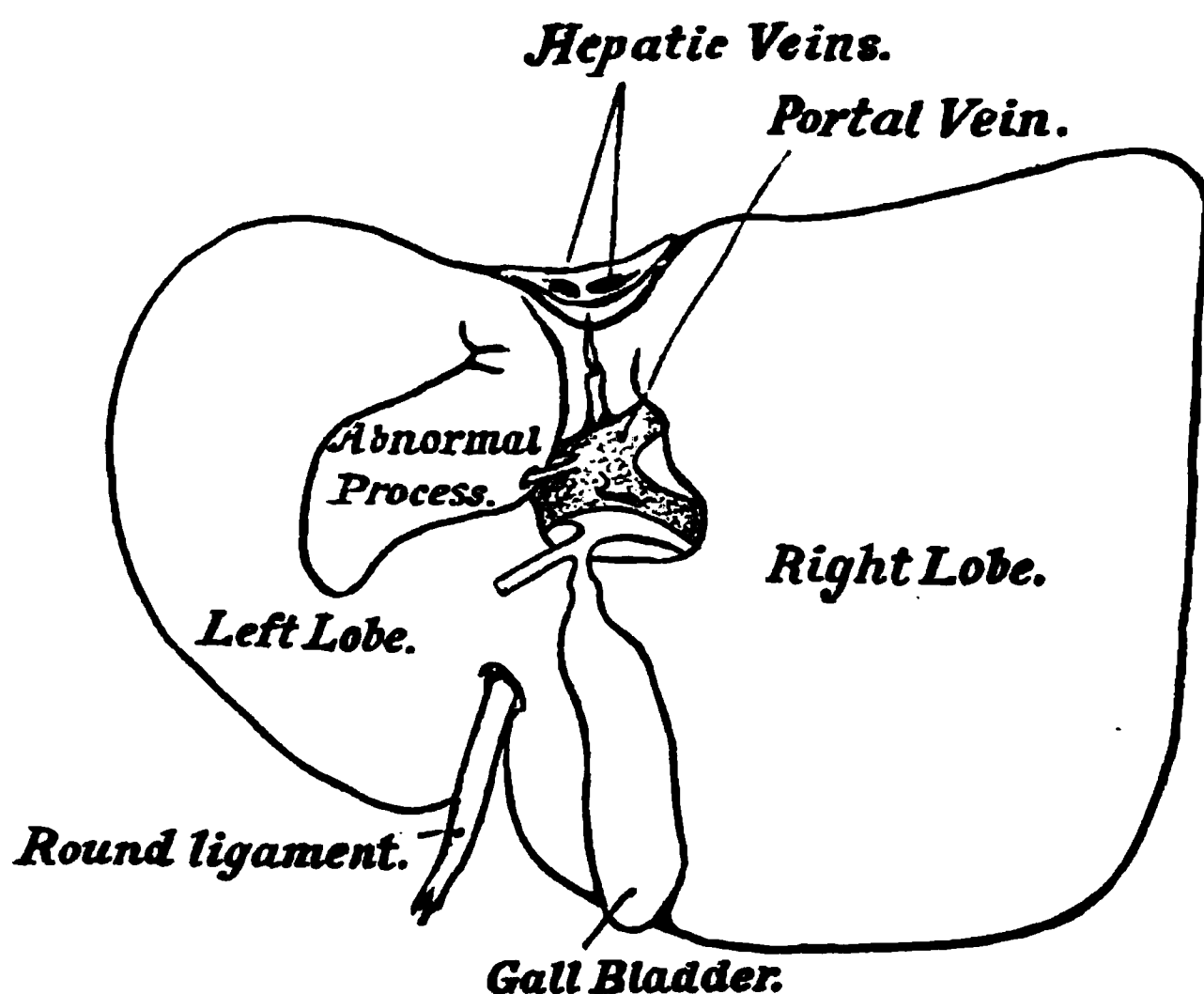


FIG. 3.—View of the liver from below and behind, showing the abnormal process growing from the left lobe. Note also the absence of the hepatic section of the inferior vena cava.

omentum was attached along the posterior part of the longitudinal fissure. The liver weighed $5\frac{1}{2}$ ozs. (156 grms.). The gall-bladder was normal in size and relations.

Remarks.—There are several points of interest about this case, the first being the fact that the child survived its birth for over fourteen weeks with a condition of heart such that no part of its body was ever supplied with pure arterial blood. To take up the heart first, the abnormalities seen here are of a very unusual kind, notably the absence of a left auriculo-ventricular aperture

Peacock, in his *Malformations of the Heart*, refers to four recorded cases in which the left auricle and ventricle failed to communicate directly. In two of these cases, of which he gives some details, the heart is described as consisting of two auricles and only one ventricle, and the left auricle communicated with the common ventricle only through the medium of the foramen ovale and the right auricle, as in this case.

Bearing in mind the fact that the existence of the rudimentary left ventricle in our case was discovered by accident, and that if the cut into the heart wall had been made only $\frac{1}{8}$ in. further forward than it was, we should have missed the cavity of the

FIG 4.—View of the liver from below and behind, showing the portal and hepatic veins and a slender fibrous cord in the position of the ductus venosus.

left ventricle altogether, it is quite possible that in one or both of the cases quoted by Peacock a rudimentary left ventricle was present. These two cases differ from ours, in that the ventricle gave origin to a single artery which gave off the right and left pulmonary arteries separately and was continued as the aorta, whereas in our case two vessels arose from the large ventricle, and indeed the pulmonary artery was larger than the aorta. Then, too, in both these recorded cases the child died on the third day, while in our case the child survived for fourteen weeks.

In the *Journal of Anatomy and Physiology* for the last ten years, though there are many records of congenital malformations of the heart, there is no instance of absent left auriculo-ventricular aperture. Physiologically the heart in this patient was bilocular, for functionally it had but one auricle and one ventricle. The arterialised blood from the lungs entered the left auricle at the same time that the venous systemic blood came through the cavæ into the right auricle. The arterial blood in the left auricle would then have been forced through the foramen ovale into the right auricle, and at the next ventricular diastole have entered the right ventricle, the rudimentary left ventricle probably not functioning at all as a cavity of the heart. The mixed blood would then pass out of the ventricle by the aorta and the pulmonary artery, that for the lower part of the body being supplied partly by the aorta and partly by the ductus arteriosus. It appears therefore that no part of the body ever received a supply of pure arterial blood except the left auricle. The latter chamber having to send all its blood through the small foramen ovale, encountered considerable resistance, and that no doubt explains the much greater thickness of the left auricular wall as compared with the right. It is possible that some provision was made for supplying the head and upper limbs with comparatively pure blood in this way: when the auricles contracted the very impure systemic venous blood would be the first to enter the right ventricle from the right auricle, then later and rather more slowly the left auricle would drive its pure arterial blood through the foramen ovale and right auricle into the common ventricle, the arterial blood lying as it were on top, and nearer to the place of exit. Before the bloods have had time to mix much, the ventricle contracts and drives the purer blood first into the aorta (and possibly the pulmonary artery), thus supplying the head and upper limbs with the purest blood possible under the circumstances.

The fact of the pulmonary artery and its branches being dilated and the ventricle being enlarged and hypertrophied, whilst the aorta does not appear to have undergone any dilatation, points to some obstruction in the pulmonary area. This obstruction is probably at the narrow foramen ovale. It is remarkable that the left auricle is not dilated.

The obstruction which must have been present at the isthmus aortæ would have contributed to the enlargement of the ventricle.

As to the origin of the anomaly, the presence of fibrous thickening and a nodule on the pulmonary and tricuspid valves suggests that the absence of the left auricular orifice is the result of an inflammatory process causing atresia.

The abdominal viscera in this child also presents several features of interest. With the exception of the stomach, which was really transposed, so that its original right side lay anteriorly instead of posteriorly, the viscera were rather in an early foetal condition than transposed. The cæcum and appendix, for example, were in the middle line and not in the left iliac fossa, as in a true case of transposition of viscera, and the large intestine was freely supplied with peritoneal covering and a mesentery.

The liver and its vascular relations presented the most interesting anomalies. The first thing that strikes one is the absence of the vena cava inferior. Owing to this, the spigelian and caudate lobes are not marked off from the right lobe. Normally the small curvature of the stomach is occupied by the tuber papillare of the spigelian lobe, but in this case apparently owing to the transposition of the stomach to the right side and the longer sweep made by the œsophagus and the cardiac end of the stomach, a lobule of liver substance was developed from the left lobe projecting into the hollow of the smaller curvature as the representative of the tuber papillare (see fig. 5). It is, however, a very well developed representative of this tuber measuring $1\frac{1}{4}$ in. by $\frac{3}{4}$ in. A similar liver was described by Professor Wardrop Griffith in 1892 (case quoted below), in which the vena cava inferior and ductus venosus were absent, and an abnormal process of liver sprang from the left lobe. In that case, however, the liver was transposed, and this process represented the spigelian lobe, whereas in the present case the process was attached to the left lobe of a normally situated liver.

It seems very doubtful whether a ductus venosus was present or not. It is true a slender fibrous cord was present between the portal and one of the hepatic veins, but it was quite impervious, and in the interior of the portal vein there was no

sign of a depression at its attachment. In a child of this age, had a true ductus venosus been present in the foetal condition, one would have expected it to be patent, or to find, at least, a considerable vestige as in the case of the ligamentum teres.

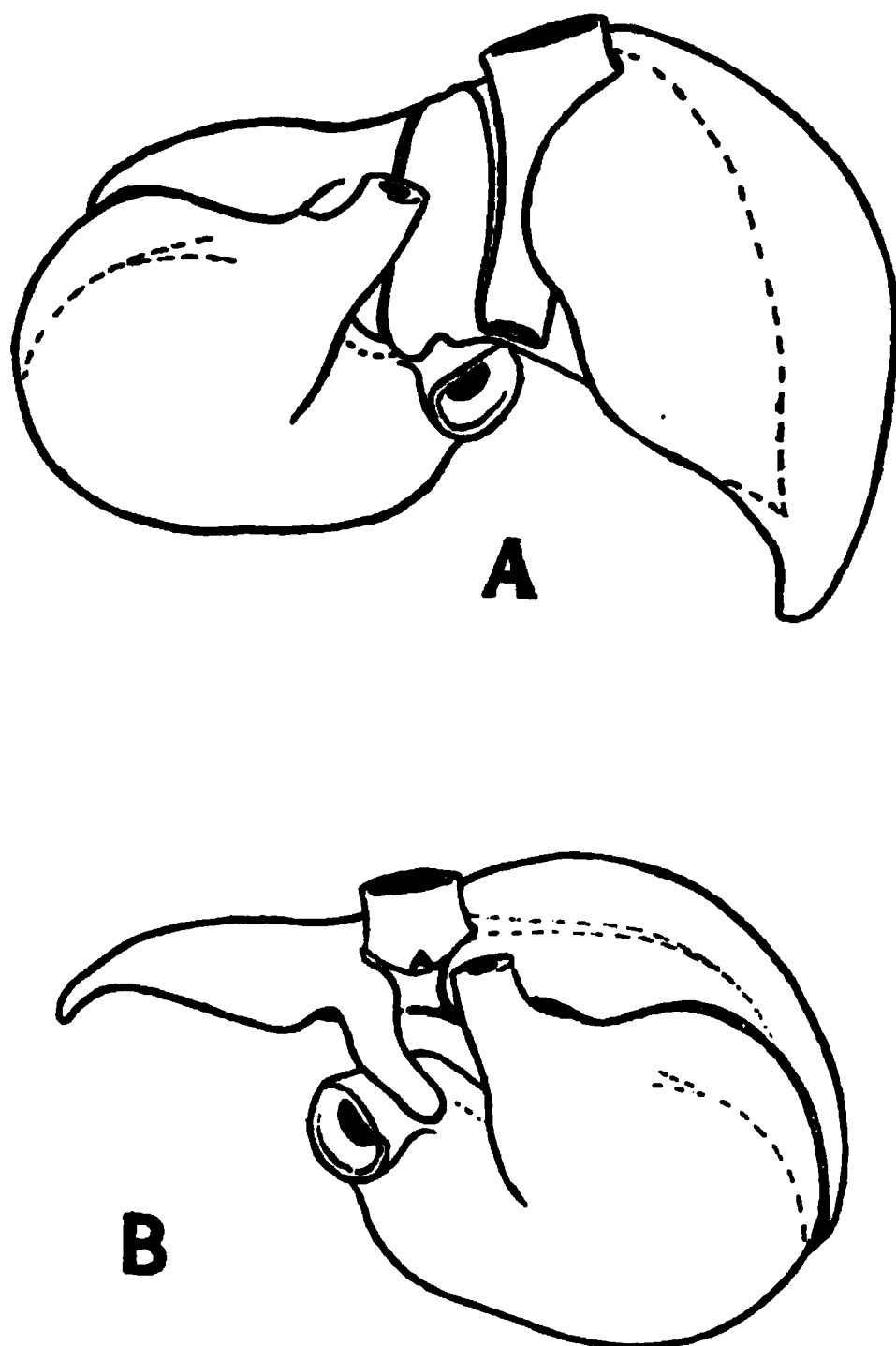


FIG. 5, A.—Semi-diagrammatic view of the liver and stomach, from His's models, showing how the tuber papillare of the spigelian lobe occupies the smaller curvature of the stomach (normal).

B.—A similar view of the liver and stomach in this case, showing how the smaller curvature of the transposed stomach was occupied by the abnormal process of liver growing from the left lobe. Note also the absence of the hepatic section of the vena cava ; also that the surface of the right lobe of the liver is more completely covered by the peritoneum than normally.

The absence of vena cava inferior and of a ductus venosus is a very unusual condition, but a similar case was recorded and carefully described by Professor Wardrop Griffith in vol. xxvi. of this *Journal* (1892).

Unfortunately the azygos veins were not examined at the autopsy, but the superior vena cava was distinctly enlarged, as though it had to convey to the heart more than its usual share of the blood.

Lastly, the absence of spleen, to judge by recorded cases, is an extremely rare occurrence. Although the spleen has been removed by operation on several occasions for disease and for injury, and the patients have recovered and been none the worse off, we have been able to find only one other instance on record where the spleen has been congenitally wanting. This was reported in the *Journal of Anatomy* for 1898-99, vol. xxxiii., as having occurred in a woman of 20, an Indian native, in whom, in spite of a most careful search, nothing resembling a spleen could be found post-mortem.

We are deeply indebted to Professor Thane for much valuable assistance and many suggestions in working up this interesting case, and in particular for the interesting hypothesis as to the significance of the abnormal process of the liver, as exemplified by fig. 5.

TWO CASES OF SUPERNUMERARY RADIO-PALMAR
MUSCLE—MUSCLE SURNUMÉRAIRE RADIO-PAL-
MAIRE OF TESTUT. By NORMAN W. KATER, M.B.,
Ch.M. Syd., *Demonstrator of Anatomy to the University of
Sydney.*

Case 1.—The muscle arose from the anterior border of the radius by a ribbon-shaped fleshy origin situated beneath the attachment of the radial head of the flexor sublimis digitorum. The muscular belly, which was flattened, and some three or four inches in length, ended in a long slender tendon which ran downwards beneath the anterior annular ligament, and was inserted partly into the common sheath of the flexor muscles of the fingers, and partly into the synovial sheath of the long flexor of the thumb.

Case 2.—The muscle in this case arose by means of a slender band-like tendon about half an inch in breadth, from the same situation on the radius as the previous case. The tendon soon became cylindrical, and extended downwards on the surface of the flexor longus pollicis. Several inches above the wrist this tendon gave place to a slender fusiform muscular belly about three inches in length; which ended in a slender tendon that traversed the anterior carpal tunnel and gained insertion into the deep surface of the central portion of the palmar fascia, at the same time being bound down by fibrous tissue to the fascia covering the flexor brevis pollicis.

The history and literature of this anomaly will be found in LeDouble's *Traité des variations du système musculaire de l'homme*, ii. p. 142 ff.

CASE OF MULTIPLE RENAL ARTERIES. By NORMAN
W. KATER, M.B. Ch.M. Syd., *Demonstrator of Anatomy to
the University of Sydney.*

THE following condition was found in one of the dissecting-room subjects during last year:—

On the right side there were five renal arteries. The first or highest arose from the aorta in the position of the normal renal artery; the second and third arose below this at intervals of one inch; the fourth began half an inch below the origin of the inferior mesenteric artery, whilst the fifth sprang from the right common iliac shortly after its commencement. There were also found three renal veins which presented the usual relation to the arteries, and two ureters, the one emerging from the upper end of the hilum, and passing downwards under cover of the upper three arteries and superficial to the lower two, the other issuing from the lower end of the hilum, and passing downwards beneath the fourth artery, but anterior to the fifth. Before entering the true pelvis the upper of the two ureters crossed the lower superficially. At the hilum of the kidney the veins, arteries and ureters presented the usual relations to one another from before backwards. In connection with the left kidney were found three arteries, one vein, and one ureter. Considering the relations from before backwards, the ureter occupied its normal position posteriorly; the upper of the three arteries was placed in a plane posterior to that of the vein, the middle artery was anterior to it, whilst the lowest was in the same plane. Both kidneys were normal in size and consistence.

For similar cases see *this Journal*, xvii. p. 250.

DESCRIPTION OF A FŒTUS AMORPHUS. By GEO. A. CHARLTON, M.D., *McGill University, Montreal.* (PLATES I.-III.)

THIS singular monstrosity was recently sent to me for the Pathological Museum of McGill Medical College, Montreal, through the kindness of Dr Boone of Presque Isle, Maine, U.S.A., in whose practice the case occurred. It was one of a twin pregnancy, full term, the patient being a French Canadian woman about 25 years of age. Nothing abnormal had marked her two previous pregnancies, either during gestation or confinement. In the present instance the woman went to full term without any abnormal manifestations. The labour was uncomplicated and uneventful up to the delivery of the first foetus, a live, well-developed normal female. The second foetus—the specimen now under consideration—came away with the placenta, to which it was attached by an umbilical cord, 20 inches in length, stated to be of the thickness of a lead pencil. Dr Boone, who examined the placenta carefully, writes that the placenta of the monstrosity was smaller than that of the normal child, and that it was adherent to it, forming a figure of 8. He states further that the normal child was in a separate sac.

The amorphous foetus was without head or upper or lower extremities. It measured 19.5 cm. ($7\frac{1}{2}$ inches) long, 14 cm. ($5\frac{1}{2}$ inches) wide, and 5.75 cm. ($2\frac{1}{4}$ inches) thick. Weight 740 grms. As the accompanying illustrations show, the general outline is oval, flattened anteriorly and posteriorly. The cephalic pole is covered by a tuft of short black hair, and is marked by four depressions. Lower down, a depression on each side corresponds to the points where the arms should have appeared. A distinct groove marks the line of the spine, the sacral portion of which, along with the pelvis, is tilted sharply to the right side. A depression marks the region of the anus, while a small bud on each side denotes where the lower extremities should have appeared. The sex is undistinguishable, a small triangular eminence arising from the upper side of a

depression beneath the pubic arch being all there is to mark externally the genito-urinary system.

The natural orifices are all closed. At the site of the umbilicus the abdominal wall is incomplete, having an oval space 2·5 cm. \times 1·6 cm. covered over by the transparent amniotic membrane of the umbilical cord. The stump of the umbilical cord contains three blood-vessels, two lateral and one central. These vessels were carefully injected in order that the vascular system might be more readily studied.

A series of photographs were now taken, showing both poles of the fœtus as well as the anterior and posterior aspects. A skiagraph revealed the fact that the fœtus possessed a fairly complete axial skeleton, the upper portion of the skull being undeveloped. With the exception of rudimentary scapulæ, the upper extremities are absent. The lower extremities are entirely wanting.

While reflecting the skin preparatory to dissection, the subcutaneous fatty tissue was found to be quite plentiful but very œdematous. A quantity of clear serous fluid oozed out from the tissue, so that after complete removal of the skin the weight of the fœtus was reduced to 175 grms., and it now measured 14·5 cm. long, 7·75 cm. broad, and 3 cm. thick. The subcutaneous tissue was plentifully supplied with minute blood-vessels. By removal of the skin, the opening in the abdominal wall at the site of the umbilicus had been considerably enlarged, disclosing an abdominal cavity lined with peritoneum but devoid of contents save the blood-vessels entering from the umbilical cord and a few masses of infiltrated areolar tissue. The muscular tissue of the fœtus was fairly well developed, so that individual muscles of the thorax, abdomen and back could be dissected out. In the upper thoracic region this muscular tissue was greatly in excess of the normal.

The vessels entering the umbilicus were dissected out: the central one proved to be the urachus and terminated as the upper portion of a pear-shaped body occupying the position of the bladder. The lateral vessels passed downwards into the pelvis on either side, following the normal course of the hypogastric arteries. At Poupart's ligament they passed backward and downward to the posterior wall of the pelvis, along which they

ascended, taking the usual course of the common iliac arteries, and uniting in the upper sacral region to form one vessel which ascended along the front of the spinal column through the abdominal cavity into the thorax, giving off along its course several lateral branches corresponding somewhat to the normal intercostal arteries.

The heart was absent. The rudimentary aorta terminated abruptly at about the point where normally the arch of the aorta should be. Several branches were given off at this point, the lateral branches passing outwards along the course of the right and left subclavian arteries, the central ones passing upwards towards the cephalic pole, simulating the vertebral and common carotid arteries. Many small subcutaneous branches emptied into the sinus at the base of the umbilical cord.

The liver, lungs, and alimentary canal were entirely absent. The abdominal and thoracic cavities were continuous one with another, the thoracic cavity being mostly filled with masses of oedematous muscular and areolar tissue.

The pear-shaped body lying in the pelvis was covered by peritoneum on its upper surface, while the lower portion was adherent to the pelvic bones below. It was filled with a clear jelly-like substance. In the right lumbar region, on the posterior wall of the abdomen, another oval-shaped mass about the size of a pea was found covered anteriorly with peritoneum. This also was hollow and filled with a similar clear jelly-like substance.

In the course of the dissection no nerves were found, and beyond ascertaining that the brain was absent, no further attempt has been made to work out the nervous system.

A study, admittedly imperfect, of the literature of this condition of fœtus amorphus has resulted in discovering no case resembling the above. Cases, it is true, are on record of similar shapeless masses of tissue, showing a stage of development much less complete—in which aberrant bony masses have been determined. The majority of the cases exhibit a lack of development of either the anterior or the posterior pole of the body. I have come across no account of an acardiac monster in which the trunk with spinal column and ribs are represented, the head and limbs being practically absent.

Journ. of Anat. and Physiology, Oct. 1901.]

[PLATE I.

Fœtus Amorphus.

DR GEO. A. CHARLTON.

Journ. of Anat. and Physiology, Oct. 1901.]

[PLATE II.]

DR GEO. A. CHARLTON.

Journ. of Anat. and Physiology, Vol. 1901.]

[PLATE III]

DR GEO. A. CHARLTON.

ACARDIAC MONSTER CAUSED BY A FŒTAL ADHESION
TO A PLACENTA SUCCENTURIATA. By EDBRED M.
CORNER, M.A., M.B., B.Sc., F.R.C.S., *Resident Assistant
Surgeon, St Thomas' Hospital.*

(Shown at the Anatomical Society, December 1900.)

THE monster that forms the subject of this paper is an absolutely unique form of the acardiac variety, due to an adhesion of the foetus to a placenta succenturiata. The specimen was obtained for me by Dr Gill, Poplar, to whom I am also indebted for data with regard to the history.

The monster was one foetus of a twin birth, the fellow of which was a female child of perfectly healthy condition. The labour took place on September 30, 1900, at full time, and being somewhat prolonged, necessitated the use of chloroform. "The placenta came away naturally about an hour after the birth of the monster. It was single and of large size." The healthy foetus was born first. "I am sorry that the nurse put it (the placenta) on the fire whilst I was attending to the mother." The father is 28 years of age and has always had good health; no history of gonorrhœa or syphilis; the mother is 29 years of age and has always enjoyed very good health, there has never been any history of uterine trouble. The parents had been married three years and have one child, a boy, and quite healthy, and 1 year and 9 months old; and a daughter, the healthy foetus of the twin birth, 3 months old. No miscarriages have occurred, and there is no history of errors in development. No cause can be ascertained to which the pathological condition found can be attributed.

In consideration of the heart of the healthy living foetus doing double work, I asked Dr Gill to examine it for signs of enlargement, etc. Three months after the birth he could detect no signs of such a condition, although that heart had done the work for both foetuses.

External appearances.—The monster is 6–8 inches in length,
VOL. XXXVI. (N.S. VOL. XVI.)—OCT. 1901. F

tinuous with the skin from the foetus; the size is about $1\frac{1}{2}$ by $1\frac{1}{2}$ inches; the attachment to the foetus is smaller than the mass, giving the tumour a pedunculated appearance.

The larger tumour, situated behind the smaller, is about twice as large and, like it, is somewhat pedunculated. It is covered for a short distance behind the groove between the two masses by amnion which ends in a fringe of membranes and is continuous with the slightly hairy scalp which covers the rest of the tumour.

The great point that is brought out by this examination is that this placenta never had any maternal attachment.

The rest of the skull is only covered by scalp, and is flattened most remarkably, giving to the monster an appearance of anencephaly, but the sella turcica cannot be felt through the scalp. When the scalp was reflected a well-developed vault to the skull was found. Under the larger of the two masses on the head a distinct hole could be felt in the roof of the skull. On careful dissection, the scalp tumour was seen to be continuous through this hole with the contents of the cranial cavity. It was also found that the tissues of both masses on the scalp were continuous with each other under the intervening groove; and was arranged, in folds, like hardened placental tissue. No extra-cranial nervous matter could be found either macroscopically or microscopically. The roof of the skull was cut away with strong scissors, being found well ossified, and the placental tissue was then found to be continuous with the brain. The latter was very small, but showed convolutions, and was much larger upon the left than the right side. The cranial cavity was also small and was markedly asymmetrical, the left being far the larger, and the right being hardly developed. It was impossible to follow the vessels from the placenta through the brain to the monster, and therefore the placenta and brain were removed in one mass.

On examining the base of the skull it was at once noticed that four vessels could be easily traced, whose description will be given later with that of the circulatory system; they were the two internal carotids, the left internal jugular, and a huge venous sinus in connection with the right cavernous sinus and the right internal jugular vein.

The Circulatory System.—Upon incising the abdomen no body cavity could be found, but in place thereof was a quantity of embryonic cedematous connective tissue. Running along the left side of the vertebral column a large vessel, the aorta, was found, which towards the pelvis divided into two branches, the

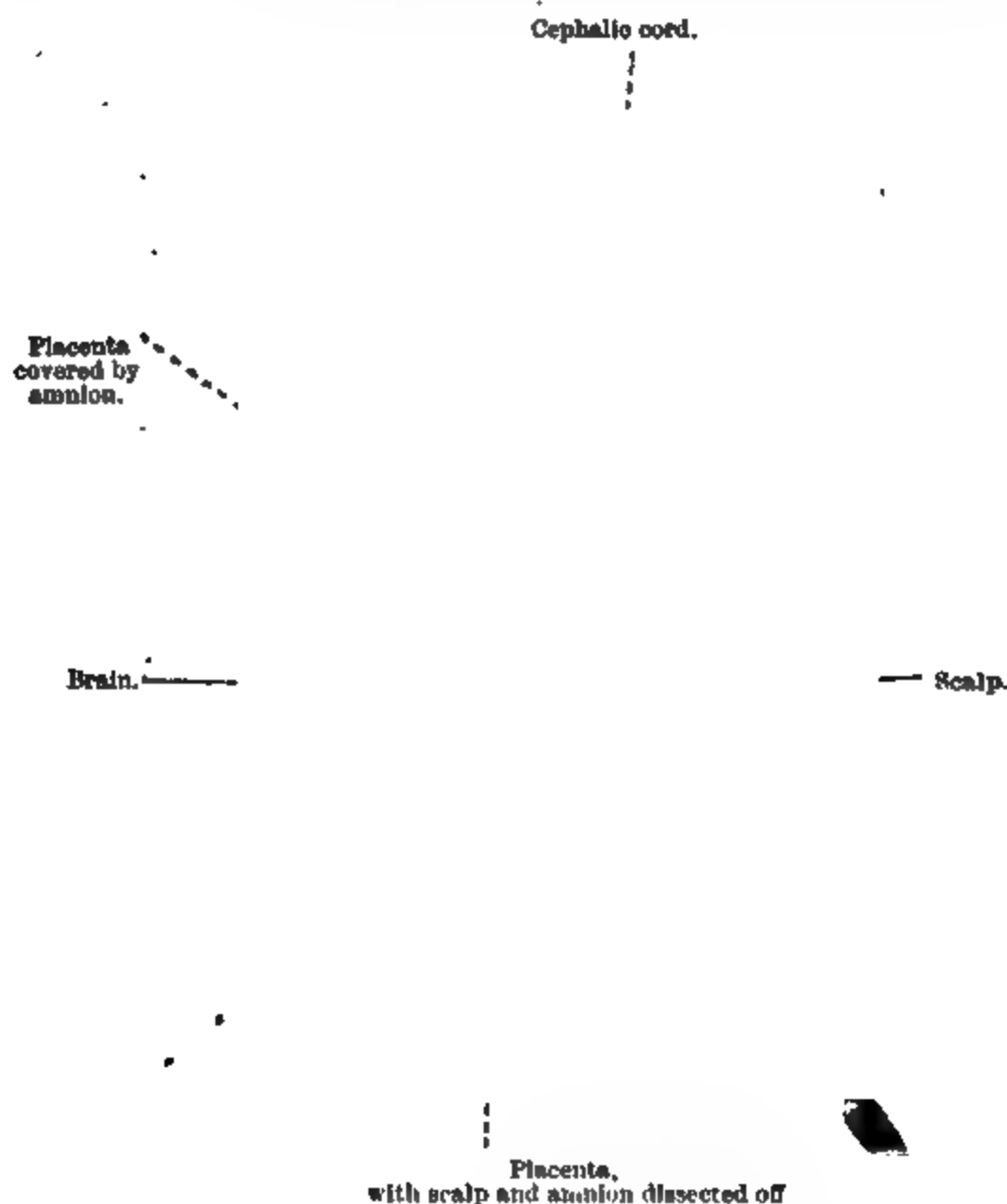


FIG. 2.—Showing placenta and brain removed in one mass, with the cephalic cord.

smaller of which, the left external iliac, passed into a mass of tissue representing the left leg; the larger curved forwards to the umbilicus, representing the internal iliac and hypogastric arteries of the left side. No traces of the corresponding arteries of the other side were discernible. On following the aorta upwards one or two branches were seen, a large one, possibly representing the

hepatic artery, though no trace of the liver was to be seen macroscopically. The aorta, higher up, divided into two vessels the common carotids, which, in their turn, again divided into external and internal carotids. The vessels of the left side were larger than those of the right; the largest of all was the left

1

2

FIG. 3.—Diagram of the circulation through the monster. 1, the three arteries forming the cephalic cord; 2, the placenta succenturiata, brain, etc.; 3, the left, and 4, the right internal carotid; 5, the left, and 6, the right external carotid; 7, the right, and 8, the left common carotid; 9, the aorta; 10, the left hypogastric artery; 10', the left external iliac artery; 11, the inferior vena cava; 12, the "composite" umbilical vein; 13, the umbilical cord of the monster containing one artery and one vein.

internal carotid, and next came the left external carotid. No signs of the subclavian arteries, heart, pulmonary vessels, and ductus arteriosus could be seen, neither was the circle of Willis in the skull found.

The venous system, like the arterial, was exceedingly simple. A sinus the size of an ordinary penholder was present at the umbilicus, where it was largest. It originated in the large venous sinus formed by the vessels of the dura mater and the cavernous and superior petrosal sinuses of the right side; piercing the basis cranii it received tributaries and increased in size until the umbilicus was reached. This vessel must represent the umbilical vein, the ductus venosus, the upper part of the inferior vena cava, the right auricle, the superior vena cava, and the right internal jugular vein. The left internal jugular vein was also present, but much smaller, and owing to the difficulties of dissection was cut across, so that its connection could not be traced.

The venous supply to the posterior end of the body consisted of a vessel on the right side of the aorta, the upper end of which ended in branches chiefly on the right side the renal veins; no connection with the umbilical vein or ductus venosus could be traced. Inferiorly the vessel curved forward and entered the umbilical cord, whilst in the cord about one inch from the body it joined the umbilical vein, as is shown in sections of the cord beyond this point, where one artery and one vein alone are present. Proximal to this two veins were visible.

Of the abdominal and thoracic viscera no trace could be found, except in the case of the bladder, which was found, as a hollow organ, in the pelvis, by the side of the hypogastric artery. The urethra ended blindly after a very short course. No trace of the midgut could be found, although its previous existence is proved by the presence of the allantois.

A well-marked buccal cavity was found, which was separated from the nasopharynx by the soft palate and posteriorly was continued into the oesophagus, which, after a short course, ended in a blind dilatation which may represent the stomach.

No sign of the larynx or trachea could be found, although a well-developed hyoid bone was present.

The nervous system was represented by a small brain, showing some convolutions, of which the right side was barely present, and a spinal cord that extended nearly the length of the vertebral column, and ended in the cauda equina.

No trace of the eye could be found in either orbit, which, like the rest of the body, was filled with oedematous connective tissue.

In a few situations definite muscular tissue was present, and the muscles of the back showed the highest degree of differentiation.

Critical.—The explanation of this condition is extremely interesting, and resolves itself into a series of problems, the first of which is that of the presence of the placenta, without any maternal attachment, upon the monster's head. The membranes that surround this placenta were macroscopically and microscopically shown to be covered with amnion on both sides, one in continuity with that of the healthy foetus and the other with the monster. Hence each foetus originally had its separate bag of membranes, and it was between these bags of membranes that the cephalic placenta arose. The placenta is not formed until the end of the third month, and up to that date the ovum is surrounded by decidua reflexa and chorionic villi. It must have been an adhesion between the two sets of membranes that led to the connection between the two foetuses. It is improbable that an adhesion between two structures which subsequently become more or less vascular could give rise to a placenta succenturiata. Hence it seems probable that an earlier adhesion was formed between the monster's head and its own membranes, so giving rise to good enough blood supply to prevent the normal atrophy of chorionic villi and so giving rise to a placenta succenturiata with amnion on both sides and without maternal attachment.

The causation of these adhesions may have been due to some endometritis of the decidua reflexa which may have given rise to both adhesions. The mother, however, has never had the least uterine trouble.

The results which have followed upon these adhesions can be followed out in some detail. The heart of the stronger of the twins will win in the battle of the blood streams, and in consequence, wholly or in part, nourish the weaker.

On examination of a section of the cephalic cord (fig. 3) of the monster, three arteries only are present, showing that the vascular connections between the foetuses consisted solely in the monster receiving impure arterial blood from its host. From the placenta succenturiata the blood was conveyed by both external and internal carotid arteries, and as the placenta

was on the left side the left arteries are larger than the right. The vascular tissue of the placenta extended beyond the adhesion under the scalp, and became connected with the brain through a hole in the vault, probably the posterior inferior parietal foramen. The possibility of the adhesion having taken place whilst the nervous system was yet on the surface of the embryo, with the resulting invagination of the brain and the subsequent development of the bony vault round the connection must be considered. Such an hypothesis seems improbable, for the original adhesion between the brain and the membranes must have been exceedingly minute to give rise to such a local adhesion later on. Hence it seems most probable that the connection between the brain and the membranes occurred later and by way of the inferior posterior parietal foramen. The result of this connection is exceedingly interesting, and a junction is established with the branches of the left internal carotid artery, which has become greatly enlarged. No such connection was formed with the branches of the right internal carotid, as is shown by the exceedingly poor development of the right side of the brain. The persistence of the right internal carotid artery must be due to its communication with that of the opposite side through the circle of Willis. The persistence of the external carotids must have been due to communications with the arteries of the scalp and the middle meningeal.¹

It is seen that the direction of the flow of the blood stream

¹ Some explanation is due for the following diversion into the region of hypothesis, and what I offer is this. If the vessels described as carotids, aorta, etc., are these vessels, then the foetus must originally have had a heart. Considering that the heart begins to develop within the first few days of foetal life, it must have antedated the formation of the pathological adhesions that gave rise to the malformation. To what stage of development the monster's heart was allowed to proceed it is impossible to say. On the other hand it can be definitely stated that the pathological adhesions took place before the end of the third month of foetal life, a time at which the heart of a normal foetus is well developed. Therefore I applied the physiology of the monster's circulation to that of a normal foetal heart, and so found reason for the atrophy of that organ in the *commotio cordis* and its total loss of function. As this occurred before the end of the third month of foetal life, six months of intrauterine existence remains, during which time it is perfectly easy for the heart to have become indistinguishable from the oedematous "connective" tissue of which the monster was chiefly composed. In fact, one argues that what happened to the rudiments of the other organs, such as the midgut, eyes, etc., happened also to the heart, viz., that it was indistinguishable macroscopically.

is reversed in both the carotids and their branches, the results of which are the poor cerebral development and the approximation of the roof and base of the skull, the non-development of the eyes, etc.

When the blood reaches the arch of the aorta, two courses will be open for it to follow, namely, to the heart or the thoracic aorta. As the greater quantity of blood is flowing down the left carotid, the stream will be mainly directed down the aorta. Some blood will escape towards the heart and enter the left ventricle, the only way out of which will be to burst the mitral valve. Similarly, some will escape down the ductus arteriosus into the right ventricle, from which it can only escape by causing incompetence of the tricuspid valve. The rest of the blood courses down the aorta and in part supplies the tissues, but mostly goes along the left hypogastric artery to the placenta common to both foetuses. The impure blood of the stronger foetus, therefore, passes through the monster and will be arterialized in the common placenta.

The problem of the venous system mainly consists in deciding the direction in which the blood flowed in the large umbilical vein. Normally this vein should return blood from the placenta to the foetus, but should this be so in the case of the monster in question, blood will be entering it both at the head and the umbilicus, the only escape pipe being the small single hypogastric artery. The other view, that the blood in the umbilical vein flows to the placenta, is supported by the fact, that the vein is smallest at the head, its origin, and increases in size as it approaches the umbilicus. If the blood flows this way, that from the head and upper regions of the trunk is conveyed to the placenta, and is the impure blood of the healthy foetus after it has been rendered doubly impure by its passage through the monster's tissues. The direction of the flow of the blood stream is reversed in the umbilical vein and ductus venosus, but is in the normal direction in the internal jugular and superior vena cava.

The blood from the posterior end of the body is collected by the remains of the inferior vena cava, and passes up a vein from the pelvic region to the umbilicus. This vein probably represents the persistence of a (left) allantoic vein.

A section through the umbilical cord of the monster shows two veins—the umbilical and allantoic, and one artery—the left hypogastric. About one inch from the body the two veins join, and only one is seen in cross-section. (See *Path. Trans.*, 1901.)

Following the course of the blood from the superior vena cava into the auricle, part will escape through the foramen ovale from the right auricle into the left auricle, where its passage through the mitral valve is obstructed by the reversed arterial flow through the aorta. The size of the pulmonary veins renders them negligible. Another portion may attempt to flow through the tricuspid valve, but will be prevented by the reversed flow through the pulmonary artery and ductus arteriosus.¹ Hence the only available outlet from the right auricle is into the inferior vena cava. At the point where the ductus venosus joins it, the blood may flow in two ways: down the inferior vena cava or along the ductus venosus. It chooses the latter, because it is the largest and the least resistant, and from this point to the level of the renal veins the inferior vena cava is practically absent, and with the umbilical vein forms a portal system originating and ending in capillaries. The blood stream in the inferior vena cava is reversed in its direction.²

The general circulatory system may be summed up as follows: blood enters the monster's head from its twin, supplying the brain, flows down the aorta, and so out of the umbilicus to the common placenta; the blood is collected from the head and upper part of the trunk by a large umbilical vein, which con-

¹ This disregards the possible presence of the undefended space connecting the ventricles. The influence of this opening will be obvious.

² The "reversal" of the blood streams may be argued from another point of view. Considering the monster at term, it has an inflow of blood at its head at high pressure from the arterial system of the healthy twin. This blood pressure must be higher than that in a monster without a heart, and is higher than that in the placenta. Hence the blood will flow through the foetus, *i.e.*, in at its head and out at its umbilicus. In an acardiac monster such as this, the blood pressure in the jugular veins and carotids will be approximately equal, and therefore the inflow of blood from the capillary system of the placenta succenturiata will have an equal choice to flow down either. This seems to be the solid ground of fact, but one comes to hypothesis when one argues that this "reversal" of the blood streams was the cause of the macroscopic signs of the originally developing heart. So that it may be truly said that it lost its heart to its healthy twin.

veys it to the common placenta; the blood from the lower end of the trunk is also conveyed to the same placenta. Therefore there is a uniform inflow at the head and outflow at the umbilicus, the monster being washed through by the impure blood of the stronger twin. It is therefore a polyp on an abnormal circulation of the twin foetus, without any existence apart from it, and died when "amputated" at birth. The blood stream is reversed in the arteries upon the cephalic side of the situation of the original heart, and normal on the other side; the converse is true of the veins.

The circulation from the stronger twin through the monster is plain. The circle is closed by the fact that there was one placenta, through which the blood was returned to the stronger foetus. The route of the circulation may be briefly stated—healthy twin, aorta, hypogastric artery, placenta succenturiata, monster's head, monster's umbilical cord, placenta, umbilical vein of healthy twin to its heart.

As at the time that the abnormal circulation was established a heart and normal circulatory system will have been established also, the physical considerations that have led to the acardiac condition of the monster are worthy of special note. As was shown above, the reversed arterial stream flowed into the left ventricle from the aorta and the right ventricle from the pulmonary artery and ductus arteriosus. On the other side of the auriculo-ventricular valves were the opposed venous streams, due to the reversed direction of the flow. Hence there was a veritable commotio cordii, with the result that the arterial and venous streams followed the line of least resistance and the heart atrophied.

In the ordinary acardiac monster, as most recently described by Dr Arthur Keith, *Trans. Obstetr. Soc.* 1900, the arterial flow is reversed on the caudal side of the heart's situation, as is also that of the veins in the same part; as the blood flows both in and out, the monster's umbilicus and the cephalic region and heart never develop. In the specimen here recorded the blood flows in the head and out the umbilicus, so that the cephalic region is the best developed. So that whilst the former is a bud *off* the circulation, the latter represents a focus *in* the line of the circulation. Another important difference lies in the

fact that in the ordinary acardiac monster the heart probably does not develop, as the cause of the acardium may act *ab initio*. In the condition when acardium develops later with a normally situated placenta, *i.e.*, after the heart has developed, the current in the abdominal aorta will be reversed, as will that in the pulmonary artery and ascending aorta, whilst it will be in a normal direction in the carotids, etc. There will be also a similar venous condition to what I have described in my specimen. Consequently there will be a similar commotio cordii that will lead to acardium. It will be nearly impossible for the foetal adhesion and abnormal placenta to be developed before the heart, and therefore it will not be considered.

In the instance that I have described, the cause of the malformation probably did not act *ab initio* but later, causing, not so much the non-development, but the atrophy of already partially developed organs. For instance the imperfect development of the brain and the absence of the eyes have been already quoted, as has also the asymmetry of the brain, for though the left side may have developed faster than the right, the latter may have atrophied. The absence of the liver is another example, for instead of receiving purified blood, it receives a small supply of doubly impure blood, whilst the major part takes the short cut through the ductus venosus. The kidneys may be further instanced. The absence of the gut forms an unequivocal example, for the presence of the allantois of the monster proves the midgut to have existed, and yet no trace could be found macroscopically. Further examples could doubtless be cited, but the above are sufficient to indicate the point.

For the description of the skeletal system and sections of the umbilical and cephalic cords, see the Pathological Society's *Transactions*, 1901.

ABERDEEN UNIVERSITY ANATOMICAL AND ANTHROPOLOGICAL SOCIETY.

IN the months of March, June, July, November, 1900, January and February, 1901, this Society held six meetings.

At the meeting in March, Dr Arthur Keith, F.R.C.S. Eng., gave a lantern demonstration on the relationships of man to the higher primates. Dr Keith first pointed out the relationships between the lower primates, anthropoids and man, with regard to the periods of life and growth, the periods of dentition, of brain growth, body growth, and sexual change. In man all these appear later and last longer than in any other animal; in the lower primates they are short and hurried, but the life periods of the anthropoids bridge the gap between the extremes. Then he showed that many adult human characters were those of foetal or infantile anthropoids; and lastly, adduced evidence for the construction of a geological history of man and the higher primates showing that it was in the miocene period that man was adapted for bipedal progression and that in the pliocene and quaternary periods the development was chiefly one of brain growth.

At the meeting in June, Mr Ian Rose, a graduate in medicine of the University, gave an address on the native tribes of Eastern Equatorial Africa, describing the chief geographical features of their country, the racial characteristics of the chief tribes, Bantu, Wanyko, Swahili, Watesta, Wakamba and Wakikuya, and gave an account of their probable descent and relationships. Mr Rose brought with him a Swahili boy who illustrated the characters of his tribe.

At the July meeting, office-bearers were elected for the next year. Professor Reid, M.D., F.R.C.S. Eng., was re-elected President, Messrs Gray, C.M.; Ledingham, M.A., B.Sc.; and Low, M.A., M.B., vice-presidents; Miss Duncan and G. G. Macdonald, M.A., secretaries. The record of abnormalities found in Practical Anatomical Rooms was then read; a specimen of supracondyloid process, numerous abnormal muscular slips and arteries showing irregular origins and distributions were exhibited.

In November the President exhibited various weapons of the Hausa people, and the medical and surgical outfit of one of their native doctors. He described the probable origin, history, physical features, manners and customs of the Hausas, illustrating his description by numerous lantern views prepared by Dr Low. The specimens shown were presented to the Anthropological Museum by Sir William MacGregor, Governor of Lagos, who sent a graphic account of the native doctor's outfit and actual practice.

Miss Margaret Duncan described the abnormal disposition of the abdominal viscera found in two female subjects. She showed the

subjects themselves, and by diagrams, etc., explained how compressive forces such as might be caused by tight-lacing acted as the sources of the mal-position.

At the January meeting, Mr Alex. Low, M.A., M.B., described the anatomy of a thirty-two days old human foetus. The specimen, kindly sent by Dr Pozzi, was extremely valuable, being in an excellent state of preservation, with membranes intact. The membranes were dissected off, and photographs were taken in various stages.

A point of particular interest, and one rarely observed in the human subject, was that the specimen showed the stage when the amnion lay in close contact with the embryo and was separated from the chorion by a large interval. The yolk sac was well developed, and the embryo measured 9 mm. in length. A complete record was given of the measurements of the different parts of the foetus and its membranes, and both the macroscopic and microscopic anatomy of the embryo were demonstrated by means of the lantern. The observations which Dr Low made were very valuable, as they served to check the inferences drawn as to the anatomy of the human embryo from investigations on the embryos of other mammals. Mr Ledingham, M.A., B.Sc., in a paper on "Finger prints," compared the results obtained from the registers of the anthropometrical department on 229 students and 169 policemen with those of Galton on 500 individuals of different races, and found they coincided in almost every detail.

At the February meeting, Miss Macdonald, Conservator of the Archæological Museum, King's College, read a paper, illustrated by numerous lantern slides, on the ancient Egyptians, their manners and customs. She mentioned the various theories put forward by different authorities as to the origin of the Egyptians, summing up in favour of those who hold that the Egyptians must have migrated from Asia and were not descended from a Nigritic stock.

After having referred briefly to the old connection between the Masai of Eastern Central Africa and the Egyptians, she discussed the character of the latter and the persistency with which their racial characteristics and type have survived through thousands of years. She then gave a sketch of the form of government which prevailed under the Pharaohs, describing shortly the social condition of the people and the high degree of excellence to which they attained in art and manufactures. She then referred to the learned professions, showing how strongly imbued the Egyptian mind was with the necessity for and beauty of learning, and closed her paper with an account of their knowledge of anatomy and medicine.

Journal of Anatomy and Physiology.

THE RELATION OF STRUCTURE AND FUNCTION AS
ILLUSTRATED BY THE FORM OF THE LOWER
EPIPHYSIAL SUTURE OF THE FEMUR. By ARTHUR
THOMSON, M.B., *Professor of Human Anatomy, Oxford
University.*

THE interdependence of Structure and Function has been universally recognised, though whether structure determines function or function originates structure, is a question about which there is much disagreement. As Mr Herbert Spencer¹ says:—"To answer this question is not easy, since we habitually find the two so associated that neither seems possible without the other, and they appear uniformly to increase and decrease together." The following observations, apart from their strictly anatomical details, appear to have an important bearing on the question above referred to.

The growth of a long bone is provided for by independent centres of ossification for the shaft and extremities. The former (diaphysis) appears long before the latter (epiphyses), and at birth, in the human foetus at least, only a few of the epiphysial centres of ossification have as yet made their appearance, and most do not begin to ossify until a very much later period. Maturity is reached when all these independent centres have fused, a process which occurs at widely different times in different animals. Meanwhile, it is important to note that throughout a considerable portion of this adolescence the bones involved

¹ *Principles of Biology*, 1898, vol. i. p. 197.

are subject to the same statical conditions; that is to say, their function as means of support is the same as that exercised by the completely developed bones. But in the earlier stages of development the epiphyses and diaphysis are still separated by a considerable layer of bone-producing cartilage. At first this layer is indefinite in form, but with the increase in size of the ossific nucleus of the epiphysis, and the extension of ossification from the diaphysis, it becomes attenuated, and ultimately forms the thin epiphysial layer which determines the form and mode of union of the epiphysis with the shaft. Throughout the period of growth the epiphyses and diaphyses are subjected to the same forces which affect them after union has taken place between them. As must be evident, the statical conditions met with in one group of animals vary greatly from those which occur in other groups. Consequently, we would expect to meet with differences in the form of the epiphysial suture, such differences as would be best adapted to withstand the strains to which the joint between the shaft and epiphyses are habitually subjected. If on examination such proved to be the case, we would have a clear instance of function determining structure.

A consideration of the following observations will, I trust, justify the correctness of such an assumption.

For the following reasons, the lower epiphysis of the femur was selected for the purposes of this inquiry:—1st, because it ossifies from a single centre; and 2nd, because in different groups of animals the femora are subjected to different strains according to the habitual posture and use of the limb. It is sufficient to refer to the bipedal method of progression as opposed to the quadrupedal gait, to illustrate what is meant.

The material at my disposal to conduct this inquiry was not great, but, thanks to the kindness of Professor Weldon, the stores at the department of Comparative Anatomy were placed at my disposal, and I have thus been able to examine a considerable number of young skeletons. I am also indebted to Professor Paterson and Mr F. G. Parsons for the loan of specimens. For the time being I have confined my observations to mammals. Of these I have examined the following:—

MARSUPIALS.—

- 1 *Didelphys Virginiana* (Virginian opossum).
- 3 *Macropus fuliginosus*.
- 1 *Halmaturus Bennetti* (Bennet's wallaby).
- 1 Kangaroo (?).
- 1 *Phascolomys platyrrhinus* (platyrrhine wombat).

7

EDENTATES.—

- 1 *Bradypus tridactylus* (three-toed sloth).

1

UNGULATES.—

- 1 *Tapirus Americanus* (Brazilian tapir).
- 1 *Equus* (horse).
- 2 *Sus scrofa* (pig).
- 1 *Capra ibex* (Alpine ibex).
- 1 *Ovis aries* (sheep).
- 1 *Ovis musimon* (mouflon).
- 1 *Cervus elaphus* (red deer).
- 1 *Cervus* (?).

9

CARNIVORA.—

- 1 *Felis leo* (lion).
- 1 *Canis familiaris* (dog).
- 1 *Canis lupus* (wolf).
- 1 *Canis vulpes* (fox).
- 1 *Meles taxus* (badger).
- 2 *Lutra vulgaris* (otter).
- 1 *Nasua narica* (white-nosed coati).
- 1 *Ursus arctos* (brown bear).
- 1 *Melursus labiatus* (sloth bear).
- 2 *Phoca vitulina* (common seal).

12

PRIMATES.—

- 1 *Presbytes Thwaitesii* (?).
- 4 *Anthropithecus troglodytes* (chimpanzee).
- 1 *Semnopithecus entellus* (entellus monkey).
- 1 *Cercopithecus mona* (mona monkey).
- 1 *Cercopithecus* (?).
- 1 *Macacus cynomolgus* (macaque monkey).
- 1 *Macacus* (?).
- 1 *Cynocephalus anubis* (anubis baboon).
- 1 *Cebus capucinus* (weeper capuchin).

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A total of 40 altogether.

As was to be expected, a great variety of outline of the epiphysial suture was displayed in the specimens examined, varieties which depend, no doubt, on the uses and strains to which the limbs are habitually subjected, such as posture, range of movement of the knee joint, and such actions as climbing, leaping, and springing. Interesting, too, are the modifications in form displayed in some aquatic mammals, where the limb is largely relieved from the strain thrown upon it as a means of support, and where the suture is better adapted to withstand the resistance opposed to it when used as a paddle or flipper.

The results obtained may best be studied by taking illustrations from individual members of a series which are more or less typical of the group to which they belong.

As a rule, the joint between the epiphysis and the diaphysis assumes the form of a series of conical projections arising from the lower end of the shaft, which are embedded in corresponding hollows on the upper surface at the epiphysis. In man's lower extremity, where the limb is mainly subjected to a vertical strain associated with the bipedal position, the joint assumes its simplest form. Here the general shape of the lower end of the femur (fig. 1, 5) is rounded from side to side, and from before backwards, so as to fit into a shallow concavity on the upper surface of the epiphysis; but if more carefully examined, the lower end of the femur is seen to be pitted centrally at the point of confluence of two shallow furrows which cross each other at right angles, and so sub-divide the joint surface into four slightly projecting areas. The upper surface of the inferior femoral epiphysis is correspondingly divided into four shallow fossæ, mapped out by a slight ridging of the surface, these ridges being arranged in harmony with the grooves on the lower end of the femur, and displaying a more or less prominent tubercle at the point where they cross; this tubercle fits into the central fossa on the under surface of the femur. The articular surfaces so described are admirably adapted to resist a vertical strain when placed in contact with each other, but are not well suited to withstand thrusts having an antero-posterior direction.

If we take as our type the femur of an animal whose limbs

are subjected to constant shocks and jars, due to its habits of

FIG. 1.—Photographs of the lower end of the femoral diaphysis and upper surface of the inferior femoral epiphysis.
1, moose; 2, red deer; 3, wolf; 4, baboon; 5, man.

leaping from rock to rock, we will find a much more complex joint between the shaft and the epiphysis. The alteration in

the character of the opposed surfaces is not only designed to withstand the sudden strains to which it is from time to time subjected, but is also well adapted to resist the habitual stress to which it is liable in a knee joint in which the upper and lower segments of the limb are united with each other in angular fashion.

Such a type is exemplified in the mouflon or wild Corsican sheep, of which a specimen is here figured (fig. 1, 1). The femur of this animal in the adolescent condition displays on its inferior extremity three pairs of cone-like projections: of these, the anterior pair are but little projecting, and are rather ridge-like than conical; the middle pair, much the most prominent, project downward, and end more or less pointedly; the posterior pair, less prominent, incline to be wedge-shaped. The inferior femoral epiphysis of this animal, the diameter of which in an antero-posterior direction is greater than its transverse width, is pitted to receive the projections from the lower end of the femur. There are thus three pairs of fossæ—an anterior shallow pair, a middle pair deeply excavated, and a posterior pair less pronounced. The middle and the posterior pair of fossæ are separated from each other by well defined lips and sharp edges. When the diaphysis and epiphysis are brought in contact, the interlocking of the surfaces described is so intimate as to withstand strains in every direction: in consequence we have, during adolescence, a joint admirably adapted to withstand the shocks incident to the habits of the animal.

It is difficult in any illustration to give an accurate idea of the complexity of the joint. To some extent, however, this is indicated by the disposition of the outline of the union of the epiphysis with the diaphysis on the surface of the bone, such as is represented in fig. 2, *a*, which is a view of the inner side of the lower end of the femur. Here the downward projection of the inner of the central pair of cones is well represented, though the degree of projection of the anterior and posterior tubercles is but little indicated by the outline on the surface. As, however, the same objection applies in all cases, the comparison of the superficial epiphysial outline forms a convenient method of grouping the specimens. As will be seen in figs. 2

and 3, the angle formed by the anterior and middle tubercles of

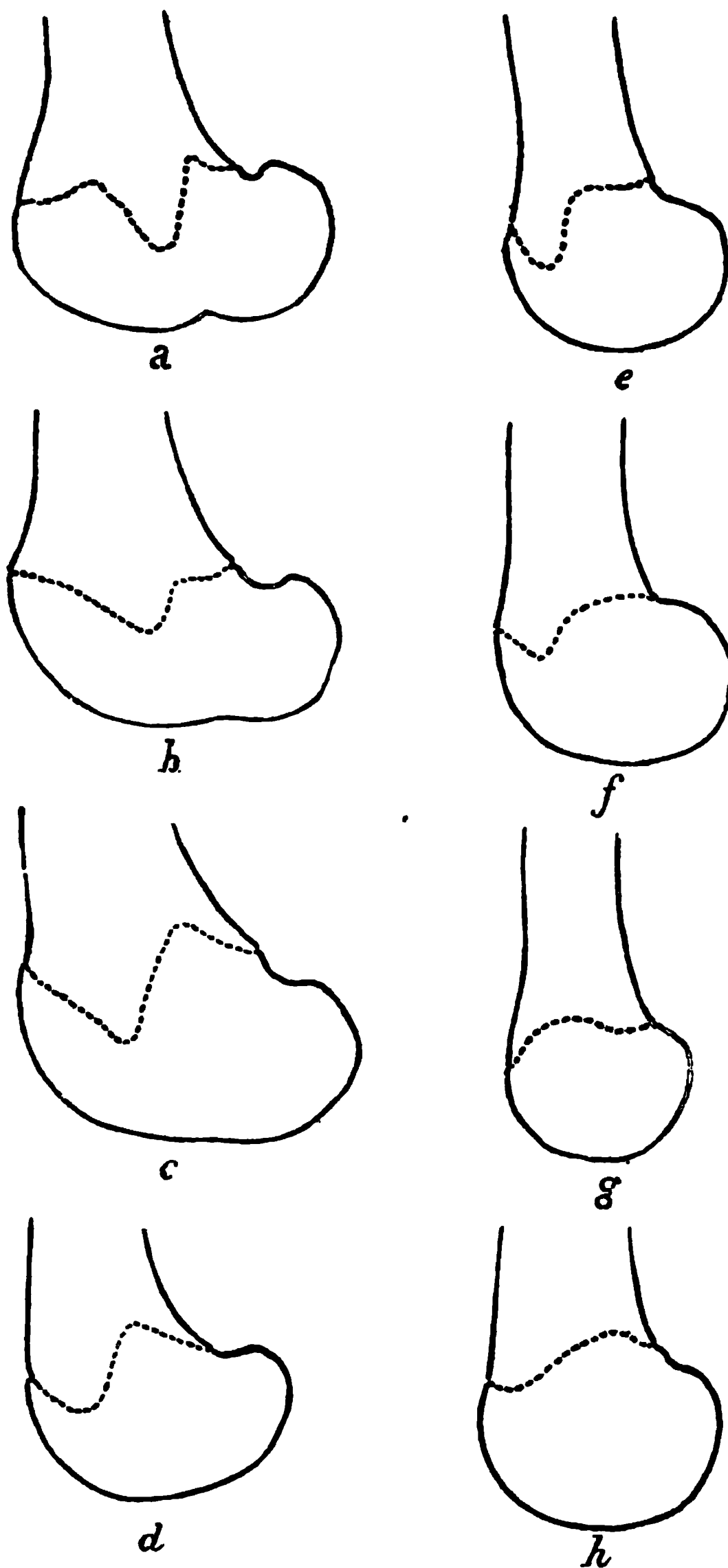


FIG. 2.—Diagrams showing the arrangement of the epiphysial line on the inner surface of the right femur in—*a*, mouflon; *b*, red deer; *c*, wolf; *d*, kangaroo; *e*, baboon; *f*, gorilla; *g*, chimpanzee; *h*, man.

the femur forms a convenient shoulder to resist the strain to

which the patellar surface of the epiphysis is subjected, whilst the condylic surfaces, which are subjected to an upward and forward thrust as they are supported on the tibiæ, are wedged in between the anterior and posterior tubercles.

Whilst it is by no means easy to group the varieties to which these epiphysial joints are subject, an intermediate type such as that represented in the wolf may be examined. This is shown in fig. 1, 3. The most noteworthy difference between this type and that already described as characteristic of the mouflon, is a reduction in the number of cones or tubercles displayed on the under surface of the femoral diaphysis: in place of there being three pairs, as in the case of the mouflon, there are only two pairs. This reduction in the number of the cones seems to be due to the disappearance of the anterior pair, or the coalescence and fusion of these with the middle pair. On the other hand, there is more equality in the size of the two pairs of cones than is the case in the middle and posterior pairs in the mouflon. The upper surface of the epiphysis displays correspondingly two pairs of fossæ of nearly equal depth; the resulting joint, whilst not possessing the same power of resistance to shock in various directions as that possessed by the corresponding parts in the mouflon, is yet sufficiently strong to meet all the requirements of such an animal as a wolf. The angle into which the tibial condyles is recessed is broad and deep, whilst the patellar surface abuts on an oblique notched area on the anterior aspect of the under surface of the femur.

A somewhat similar pattern is displayed in the Cervidæ (fig. 1, 2), though here the patellar slope is more extensive than in the wolf, and the recess into which the tibial parts of the condyles fit less deep.

As we pass to forms in which the range of extension of the knee is much increased, as evidenced by the confluence of the patellar and tibial surfaces, we find the whole epiphysis undergoing an antero-posterior compression, so that its transverse diameter now much exceeds its antero-posterior width. Correspondingly, there is an alteration in the form of the lower end of the femoral shaft.

I have taken as a type of this variety the forms displayed in the femur of a baboon (fig. 1, 4). There the lower end of

the bone displays four blunt wedge-shaped processes, differ-

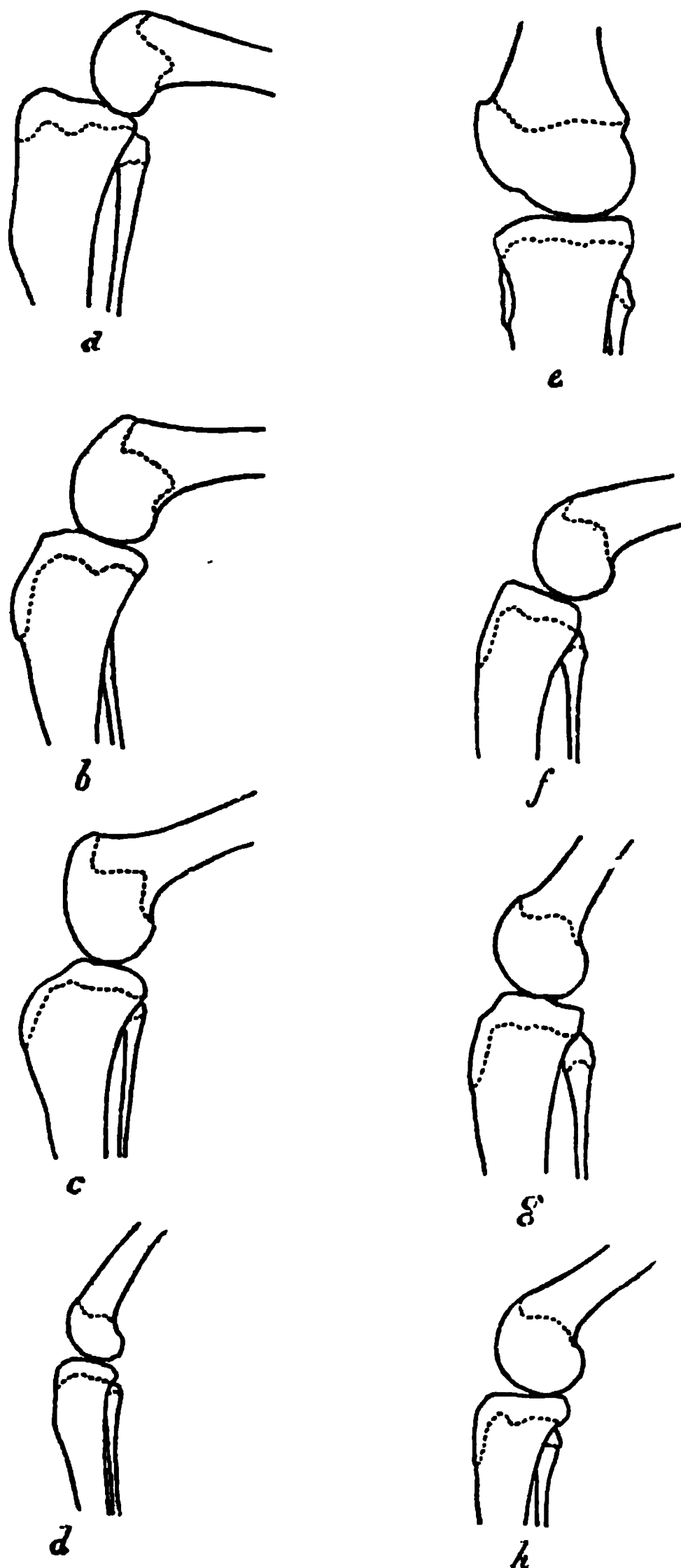


FIG. 3.—Diagram to show how the arrangement of the epiphysial joint at the lower end of the femur is modified as the range of extension of the knee joint is increased. *a*, kangaroo; *b*, polar bear; *c*, lion; *d*, wallaby; *e*, elephant; *f*, entellus monkey; *g*, chacma baboon; *h*, gorilla.

ing much in their projection from those already examined.

yet still displaying a conformity to the general type in that they are arranged in pairs. There are two pairs, and the anterior pair do not differ much in their development from the posterior pair. The upper surface of the epiphysis in general outline and shape is remarkably like that in man, but on closer inspection the fossa with which it is pitted are deeper and more clearly separated by upstanding crests than is the case in the human femur.

Unfortunately, the specimens of anthropoids at my command do not enable me to represent what, there is every reason to believe, would be an intermediate type between the baboon just described and man. I am only able to figure the lower end of the femur of a chimpanzee (fig. 2, *g*), in which, unfortunately, the ossification is not sufficiently advanced to give the precise and definite forms displayed in the other specimens.

Of interest are the modifications displayed in the form of the epiphysial suture in mammals of aquatic habits. As a type of this class, the femur of the seal may be taken. Here the lower end of the femur is much compressed antero-posteriorly, and the inferior surface of the diaphysis is divided into two rounded tubercles, separated mesially from each other by a fairly well marked antero-posterior furrow: slight evidence of a further subdivision of these tubercles into anterior and posterior parts may be observed, but for all practical purposes may be disregarded, so feeble are the indications of any such separation into pairs. Mention is made of the fact, however, as tending to display a conformity to the more general type, which has here undergone modification to a simpler form. The upper surface of the epiphysis displays a pair of fossæ in conformity with the tubercles of the shaft, and the suture between the two is such as best to withstand a side-to-side strain, but ill adapted to withstand a force acting parallel to the axis of the shaft of the bone, or a strain in an antero-posterior direction. An examination of the skeleton of the hind limb of the seal proves that the strains to which it is most subjected in action are just those which this suture at the lower end of the femur is best calculated to withstand.

In the elephant, in which the hind limb is straighter than in most other mammals, the epiphysial joint, subjected as it is to

a vertical strain, is simpler in its form and resembles more closely the arrangement displayed in man than is ordinarily the case in the quadrupedal type (fig. 3, *e*).

In the sloths, a group of animals in which, on account of their arboreal habits, an entirely different kind of strain is thrown on the limb, we would naturally expect to find a modification in the form of the epiphysial suture; nor in this are we disappointed, for in the specimen which I exhibit we find a remarkable difference in the form of the opposed surfaces from that which we have hitherto examined. In these animals there is a complete reversal of the arrangement already described; for in place of the lower end of the femur being tubercular, it is pitted, displaying two well marked hollows on either side of the middle line, the sides of these fossæ being channelled by a series of irregular grooves. On the other hand, the upper surface of the epiphysis, instead of being hollow and pitted, is elevated on either side over each condyle into irregular fluted projections, which fit into the corresponding recesses on the under surface of the femoral shaft. The resulting suture withstands admirably strains directed against it in all directions; but it is obvious that during the life of the animal it is more subject to a tearing than a crushing strain, as is the case in most of the types already referred to.

From a consideration of the foregoing facts, it seems to me that we are left with no other conclusion than that the form of the epiphysial suture is determined by the function of the limb; and since that function is exercised during a period of life in which the structure is still undeveloped and incomplete, we have a clear case, at least in this instance, of structure being determined by function.

Note.—Since the above was written, I have had an opportunity of examining a number of other specimens. The results, however, are entirely confirmatory of my previous conclusions.

THE FORM AND FORM-RELATIONS OF THE HUMAN
CEREBRAL VENTRICULAR CAVITY. By J. O.
WAKELIN BARRATT, M.D., B.Sc. (Lond.), F.R.C.S. (Eng.),
Pathologist to the West Riding Asylum, Wakefield. (PLATE
IV.)

BUT few observers have studied the form of the ventricular cavity of the cerebrum, that is to say, of the third and lateral ventricles. The only published illustrations appear to be those of Welcker,¹ Testut,² and Retzius,³ all representing casts of dilated ventricles. The first are not wholly correct; for example, the distance between the anterior cornua, corresponding to the septum lucidum, is represented as about ten to twelve millimetres. Testut's cast is better than Welcker's, but the models of Retzius are the most perfect and the most delicate. The illustrations given should be compared with figs. 10 to 14. None of these authors describe the relations of the form of the ventricular cavity to that of the cerebrum.

The necessity of obtaining some exact data, in order to be able to study more accurately the alteration in form which the cerebral ventricles undergo in the atrophy of the brain, which is so commonly seen in patients dying in asylums, led to the present work being undertaken.

It is not possible to determine the form of the healthy or extremely slightly dilated cerebral ventricles by any method which has for its object the preparation of a cast, for the filling of the ventricles with plaster of Paris or other material is only partial, and of necessity alters the form of the ventricles to which it penetrates, while the fragility of the resulting cast prevents its removal without fracture.

The only method giving exact results, and at the same time enabling the form-relations of the ventricular cavity of the

¹ *Virchow's Archiv*, Bd. 74, 1878. Reproduced in *Quain's Elements of Anatomy*, 10th edit., vol. iii. pt. i. p. 126.

² *Traité d'Anatomie humaine*, Paris, 1900, 4me édit., Tome ii. p. 704.

³ *Biologische Untersuchungen*, neue Folge, ix. SS. 45-49, Stockholm, 1900.

cerebrum to be accurately determined, appears to be that of reconstructing the ventricles from a series of sections, the position and appearance of which is carefully recorded. The best way of accomplishing this is, not by means of frozen sections of the head, for this causes deformity and artefact appearances,¹ but by having recourse to sections of hardened brain.

The procedure adopted in the present research was the following: a brain was selected which was well formed, and exhibited a very slight degree of wasting, as evidenced by the existence of a little fluid in the sub-arachnoid space. It was thought preferable to choose a brain in which the ventricles contained a small amount of fluid rather than a perfectly normal one, because if the ventricular walls are separated very slightly from each other, instead of being in contact, as they frequently are in quite healthy hardened sections, the limits of the ventricular cavity can be readily recognised by the naked eye, whereas the complete apposition which occurs in ventricles free from fluid would necessitate the making of microscopic sections to determine the exact limits of the ependyma. In fact, even in the case of very slightly dilated ventricles, microscopic sections are necessary to determine the form of the inferior cornua, the walls of which in the middle portion of their extent usually come in contact even in dilated ventricular cavities.

The brain selected, that of a female dement, 40 years of age, was fairly well formed, had a cerebral index of 81, and exhibited only a slight degree of atrophy of the brain mantle. It was carefully removed, and was placed at once, without being incised or the membranes stripped, in a saturated solution of potassium bichromate, in which it at first floated, slowly sinking at the end of one or two days, but remaining nearly of the same specific gravity as the bichromate solution, for a length of time sufficient to allow a well defined hardness of the surface to occur. By this method of hardening a minimum change of form is induced. It cannot be asserted that absolutely no alteration of the shape of the brain occurs, for the support of a liquid is probably not identical with that of the skull and dura

¹ Cp. Froriepe, *Anat. Anzeig.*, Bd. xix. SS. 427-443.

mater; but such alteration as occurs is presumably small, and certainly no readily recognisable change of shape takes place.

After hardening was completed, sketches of the outline of the brain and its principal sulci were made to scale (figs. 1, 2, 3).

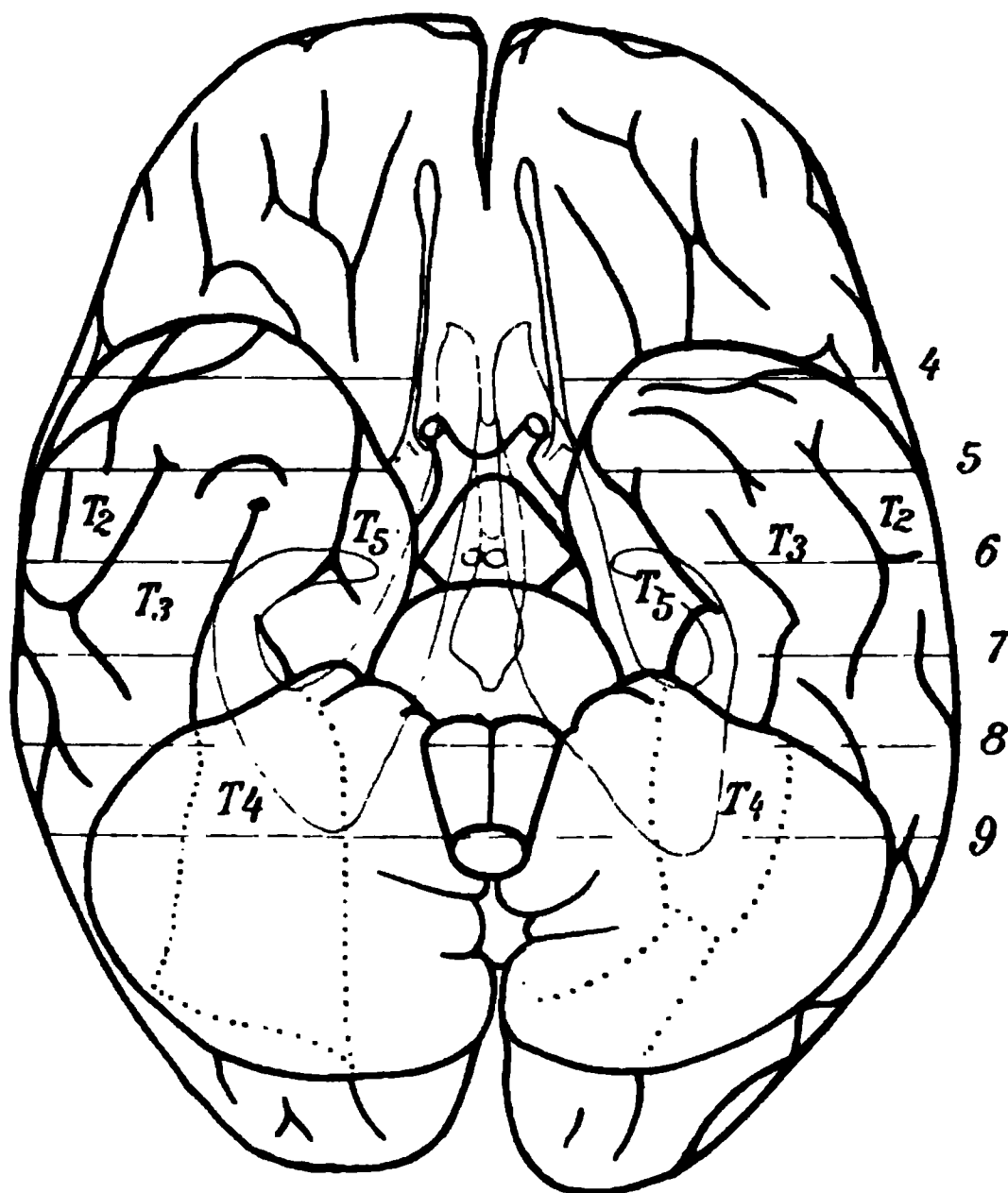


FIG. 1.—Plan of the brain viewed from below, the principal sulci and the temporal convolutions being indicated, and the outline of the cerebral ventricular cavity being inserted *in situ*. The hemispheres are not quite symmetrical, the tips of the frontal occipital and temporal lobes passing farther forwards on the right side than on the left. A corresponding asymmetry is noticeable in the lateral ventricles. Note particularly the relation of the anterior cornua to the tips of the temporal lobes, and also the position of the extremities of the inferior cornua in respect of the latter. The extent to which the posterior cornua pass backwards towards the tips of the occipital lobes should also be noted. In this and the two succeeding figures the frontal planes 4 to 9 indicate the situations in which the sections shown in figs. 4 to 9 are made. The figs. 1 to 9 are all drawn of one-half the natural size.

During this and all subsequent procedures every care was taken to avoid injuring the brain, drying its surface, or leaving it so little supported that its form might undergo alteration.

The brain was then sectioned in vertical transverse plane at

intervals of twelve and a half millimetres (figs. 1 to 3). The slices, as they were cut, were placed in bichromate solution, and a tracing of each was made without delay. With the aid of these tracings, the sketches of the cut surfaces given in figs. 4 to 9 were obtained. The slight differences which were met with between the sketches of the cut surfaces and of the whole brain (figs. 1 to 3) were halved in subsequently preparing the model of the ventricles.

In order to be able to reconstruct the ventricles from the sections, it is necessary to have two planes marked out on each section, one horizontal and one sagittal. The former was obtained by placing the brain, before section, in a frame, by the aid of which an incision was made all round its outer surface in the horizontal plane indicated by the unlettered line in figs. 2, 4, 5, 6, 7, 8, 9. [In figs. 10 to 13 this plane is omitted, but by reference to the preceding figures its position is readily ascertained, particularly in fig. 10.] The second plane was the mesial plane of the brain, indicated by the great longitudinal fissure and the structures in the middle line at the base of the brain.

These two planes being known, a plan and front and side elevations of the cerebral ventricular cavity were readily made. The former is inserted *in situ* in figs. 1 and 3, and a side elevation of the third and the left lateral ventricles is given in fig. 2.

The plan and elevations were then copied upon a block of wood, and by their aid and that of figs. 1 to 9 a carving was made of the ventricular cavity of the cerebrum. The model thus obtained (figs. 10 to 13) was necessarily not quite so delicate as was required by the sections, the ventricular cavity being in some places of extreme thinness, owing to the close approximation of the opposed surfaces of its lining membrane. In making the model of the cerebral ventricular space, recourse was had to numerous sections and dissections both of fresh and hardened brains, and much guidance was afforded by a study of plaster casts of dilated ventricles.

Only a single well formed brain was used for the reconstruction of the ventricles, so that no general statement can be made as to the nature and extent of the variations of the form and form-relations of the cerebral ventricular space in other brains. These and allied inquiries would, even if time had permitted

them to be undertaken, have extended the investigation far beyond the limits originally laid down, while the results so far achieved have up to the present fulfilled the want which led to this work being entered upon.

In its general form the cerebral ventricular space is shown by the model (figs. 10 to 14) to be delicately constructed, its thickness being in all parts very small. It consists of a mesial piece, approximately triangular in outline, representing the

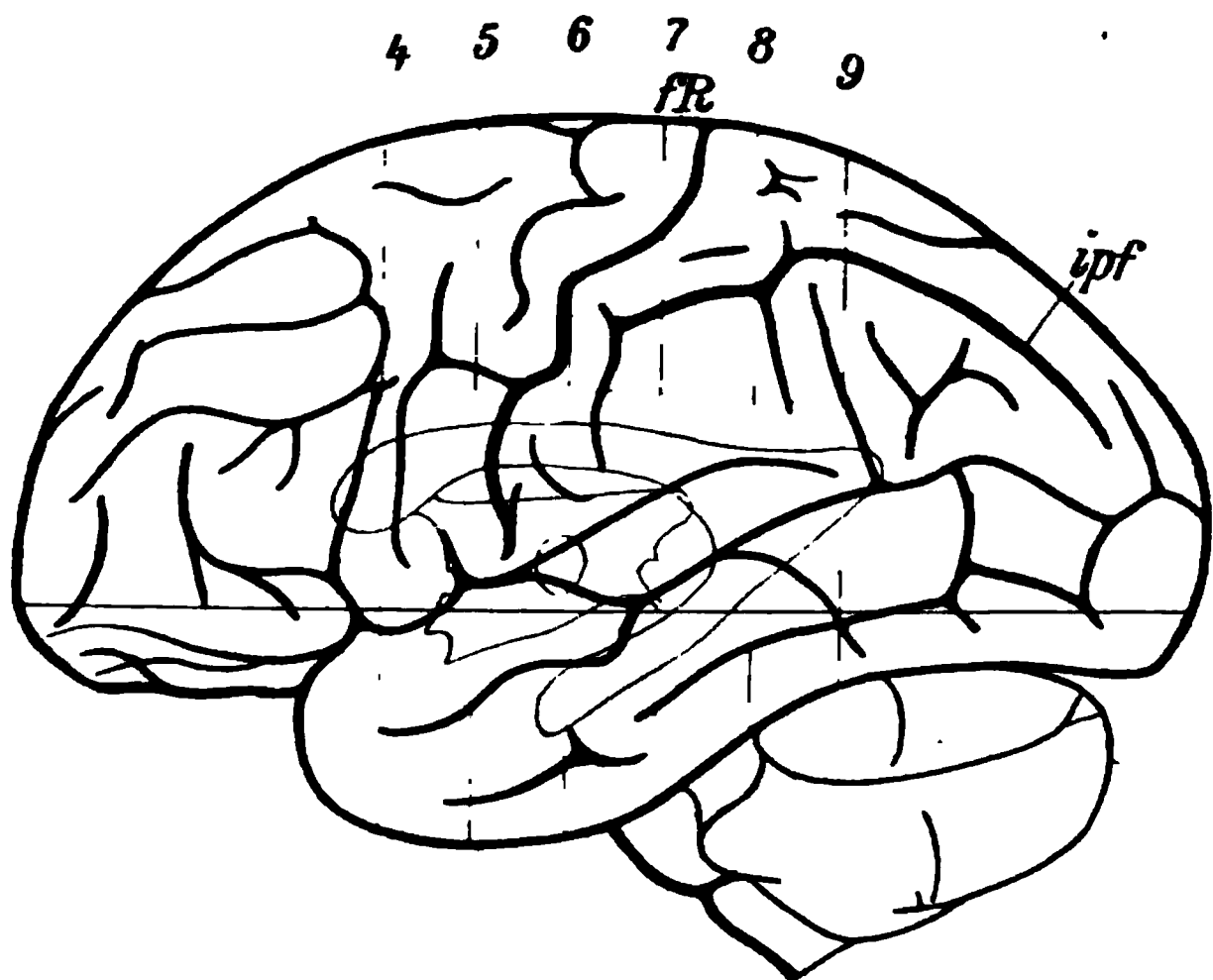


FIG. 2.—The brain seen from the side. The relation of the third and left lateral ventricles to the frontal, parietal, temporal, and occipital lobes should be noted. Observe also the situation of the lateral ventricle in respect of the fissures of Rolando and Sylvius and the intra-parietal fissure, and further, in reference to the central and first and second temporal gyri. The unlettered horizontal line corresponds to the horizontal plane, similarly indicated in figs. 4 to 9, which was marked out on the outer surface of the brain in order to enable the horizontal level of the sections to be known.

third ventricle, which is connected anteriorly on each side with the lateral ventricular cavities. Each of the latter consists of a flattened body running nearly horizontally from before backwards, with some lateral obliquity, and prolonged in front below and behind into flattened curved expansions, known as the anterior, inferior, and posterior cornua respectively. When free from dilatation the ventricular space is made up of little more than a complex of curved and flattened surfaces; and in the brain

selected. the edges of the bodies of the lateral ventricles and the middle portions of the descending horns were found to be almost of paper thinness. The space occupied by the model was 8 c.c., but the actual ventricular content was probably little more than half this amount, the larger size of the former being partly from the difficulty of obtaining the necessary thinness of its segments and at the same time preserving the integrity of

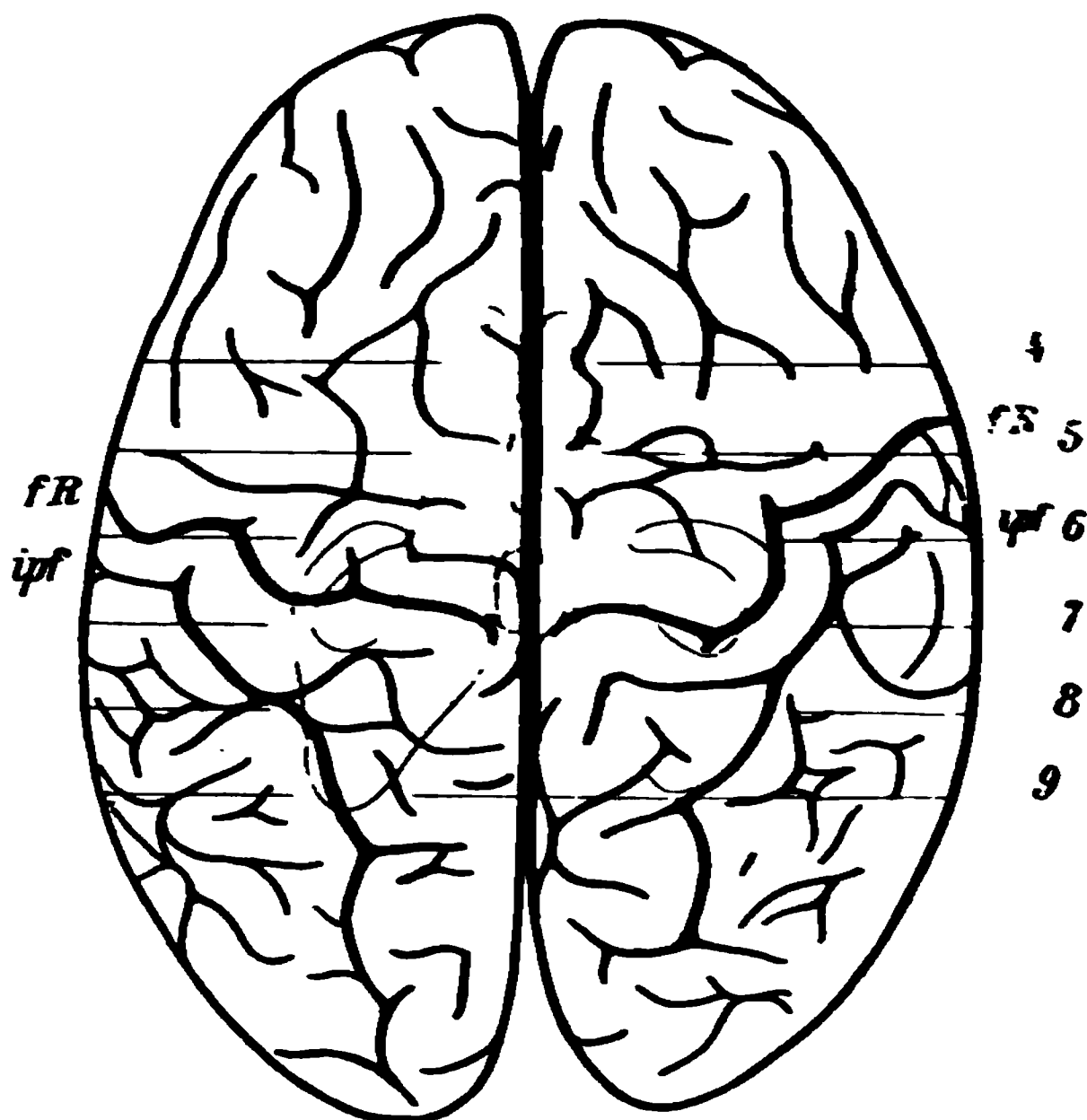


FIG. 3.—View of the brain from above. The asymmetry seen in fig. 1 is again recognisable. Note the position of the third and lateral ventricles in respect of the Rolandic and intra-parietal fissures.

the whole, and partly from the omission to indicate the grooving caused by the choroid plexuses.

As regards the general form of the cerebral ventricles, the first point to be referred to is the absence of perfect symmetry of the lateral ventricles. This is most marked in the right posterior cornu (compare figs. 10 and 14, and also 9), the tip of which does not extend as far posteriorly (figs. 1 and 3) nor reach so high as that of the left, and is consequently much more obtuse than its fellow. The right posterior horn also is

slightly turned inwards, while the left is directed a little upwards and outwards.

Similarly, there is a difference in the width from side to side of the bodies of the lateral ventricles (figs. 1 and 3), the left being the broader. This difference in breadth is accompanied by some alteration in the shape on section of the bodies of the lateral ventricles (figs. 5, 6, 7).

The inferior cornua exhibit differences in their width from side to side (figs. 1 and 3), the right being the larger. There is

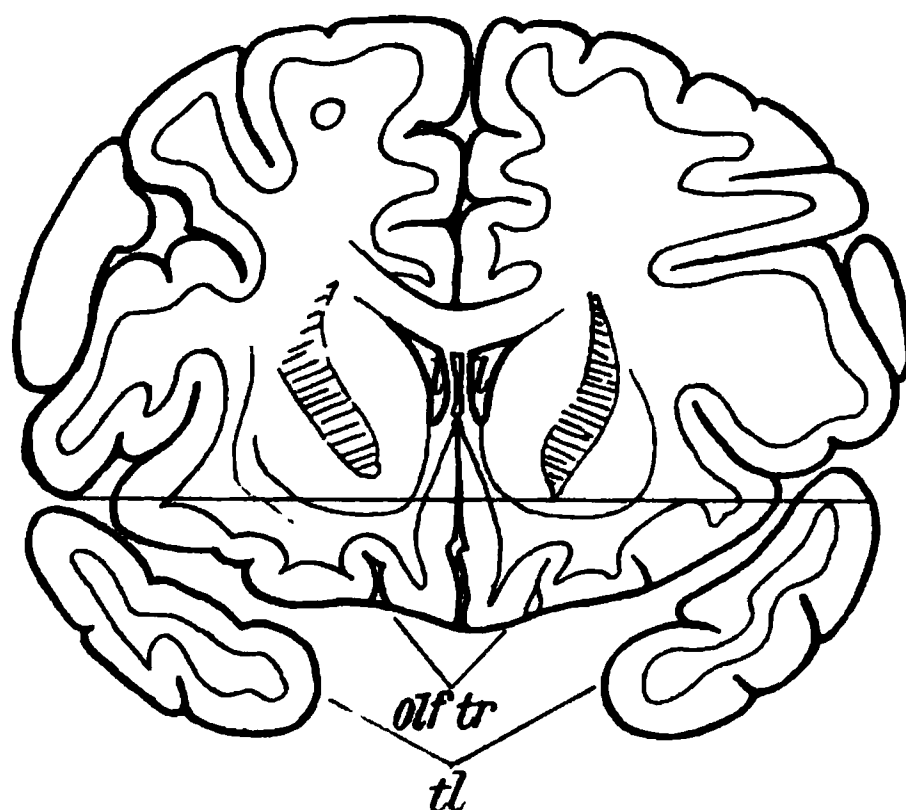


FIG. 4.—Frontal section of brain in the plane 4, figs. 1 to 3, passing through the frontal lobes and the tips of the temporal lobes, *tl*. The anterior cornua, *l.l.*, are seen lying below the corpus callosum, separated from one another by the septum lucidum, the cavity of which is shown. External to the anterior cornua the caudate nuclei are seen, and still more externally the lenticular nuclei, with the anterior limb of the internal capsule intervening. The olfactory tracts, *olf.tr.*, are also included in the section. The right side of the section lies to the right in the illustration, and the left to the left. The same is true of figs. 5 to 9.

also some difference in curvature, the right making a bolder sweep than its fellow, and consequently extending further outwards (figs. 10 to 13).

The anterior cornua are more nearly symmetrical. They reach forwards to the same extent, but the right is seen to be slightly wider from side to side, especially when viewed from before (fig. 11).

In respect of the causation of the asymmetry of the ventricular space, the question arises, how far is it due to

asymmetry of the brain? Now, in the brain selected, which, as already stated, appeared well formed, there was nevertheless, after hardening, slight asymmetry recognisable (figs. 1 and 3); the right hemisphere, as a whole, was slightly in advance of the left, a difference noticeable in the tips of the occipital and temporal lobes, and to a less degree, of the frontal lobes

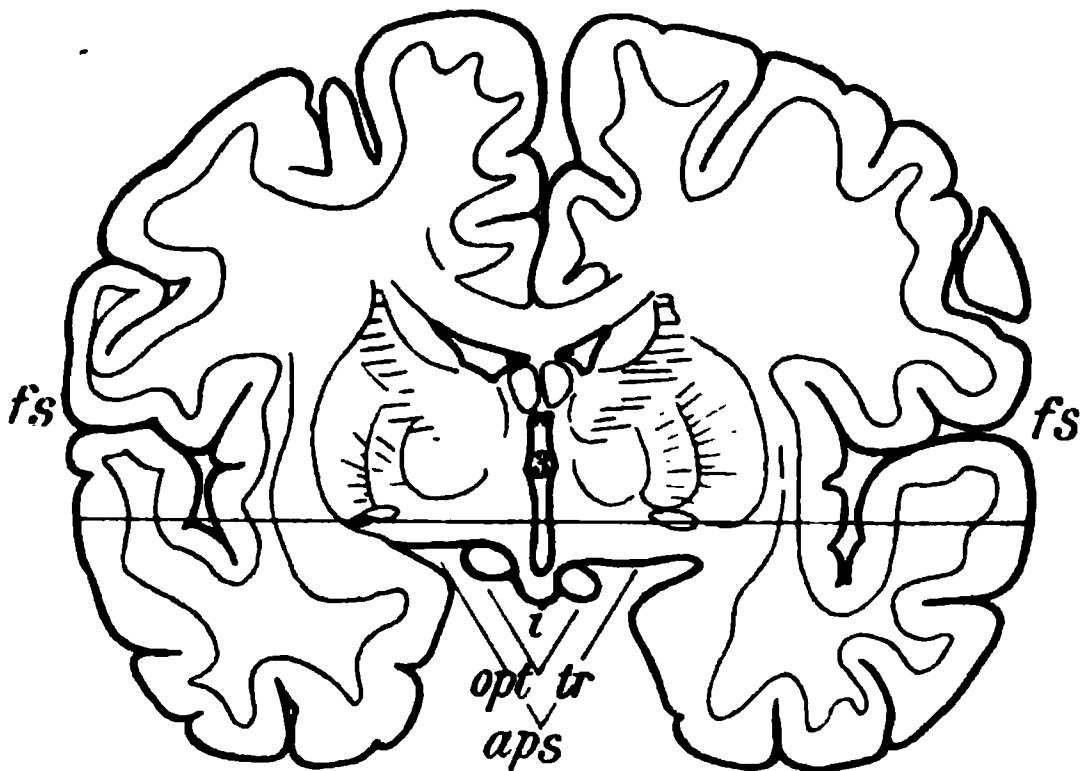


FIG. 5.—Frontal section of brain in the plane 5, figs. 1 to 3, passing through the infundibulum, *i.*, just behind the optic chiasma. The bodies of the lateral ventricles, of unequal size and shape, are seen lying below the corpus callosum on each side of the middle line, separated from the third ventricle, 3, by the pillars of the fornix. The under surface of the body of each lateral ventricle is in contact with the caudate nucleus externally, and the tænia semicircularis and adjoining portion of the optic thalamus internally. The inner border comes into relation with the choroid plexus and the fornix. In the middle line the third ventricle is cut in front of the middle commissure; it has on each side, above, the anterior end of the optic thalamus, and below comes into relation with the olfactory field, *a.p.s.*, the internal capsule and the lenticular nucleus; its outer surface presents a horizontal ridge on each side, which indicates the separation between these two portions. Below the lenticular nucleus the anterior perforated space is seen, and externally the island of Reil, with the posterior limb of the fissure of Sylvius leading to it. Between the lenticular nucleus and the anterior perforated space the anterior commissure is seen cut across.

also. A corresponding slight asymmetry of the middle fossæ at the base of the skull was also noticeable. It follows, therefore, that the asymmetry of the ventricular space of the brain examined is, in part at any rate, dependent upon asymmetry of the cerebrum. But it does not follow that this ventricular asymmetry is exclusively related to asymmetry in the general form of the cerebrum, for other factors may act

as determinants of the form of the ventricles. Thus the infolding of the brain mantle was, as is frequently the case, not perfectly symmetrical on the two sides, and the possibility of unequal development of corresponding regions of the two hemispheres is also to be borne in mind. The determination of the extent and degree in which asymmetry of the ventricular space is related to asymmetry of the cerebrum (and cranium) would obviously require, at any rate when existing in only slight degree, as in the present case, the very accurate preparation of hardened sections of many brains, accompanied by observations of extreme minuteness. It is not unlikely, however, that, independently of the development of the brain, the limits of the cerebral ventricular cavity may vary, for we have here to do with a vestigial structure the degree of regression of which may conceivably be unequal in different cases.

The relation of the form of the cerebral ventricular space to that of the various components of the brain will be referred to later, when the ventricles are described in detail. A few general features may, however, be now noted.

The third ventricle lies in the thalamencephalon, coming below into close relationship with the structures at the base of the brain. The optic chiasma roughly represents the position of its anterior limit when the brain is viewed from below (fig. 1). Its posterior limit lies vertically a short distance in front of the lower border of the pons Varolii (figs. 1 and 2).

The lateral ventricles are deeply seated. The bodies of the ventricles lie on each side close to the middle line (figs. 1 and 3), immediately below the corpus callosum (figs. 4 to 7).

The anterior cornua extend forwards but a very short distance in the frontal lobes (figs. 1 to 3); they reach to about forty-five millimetres from the anterior extremity of the brain, their tips lying approximately as far forwards as those of the temporal lobes. The anterior cornua lie close to the middle line, the maximum distance between their outer borders being about fourteen millimetres.

The inferior cornua lie within the temporal lobes, ending about twenty-nine millimetres behind the tips of these lobes

(figs. 1 to 3). They are situated nearer the inner border than the outer surface of the temporal lobes, and their anterior limit is just in front of the corpora mammillaria, and corresponds to the anterior portion of the middle commissure of the third ventricle (figs. 2 and 10).

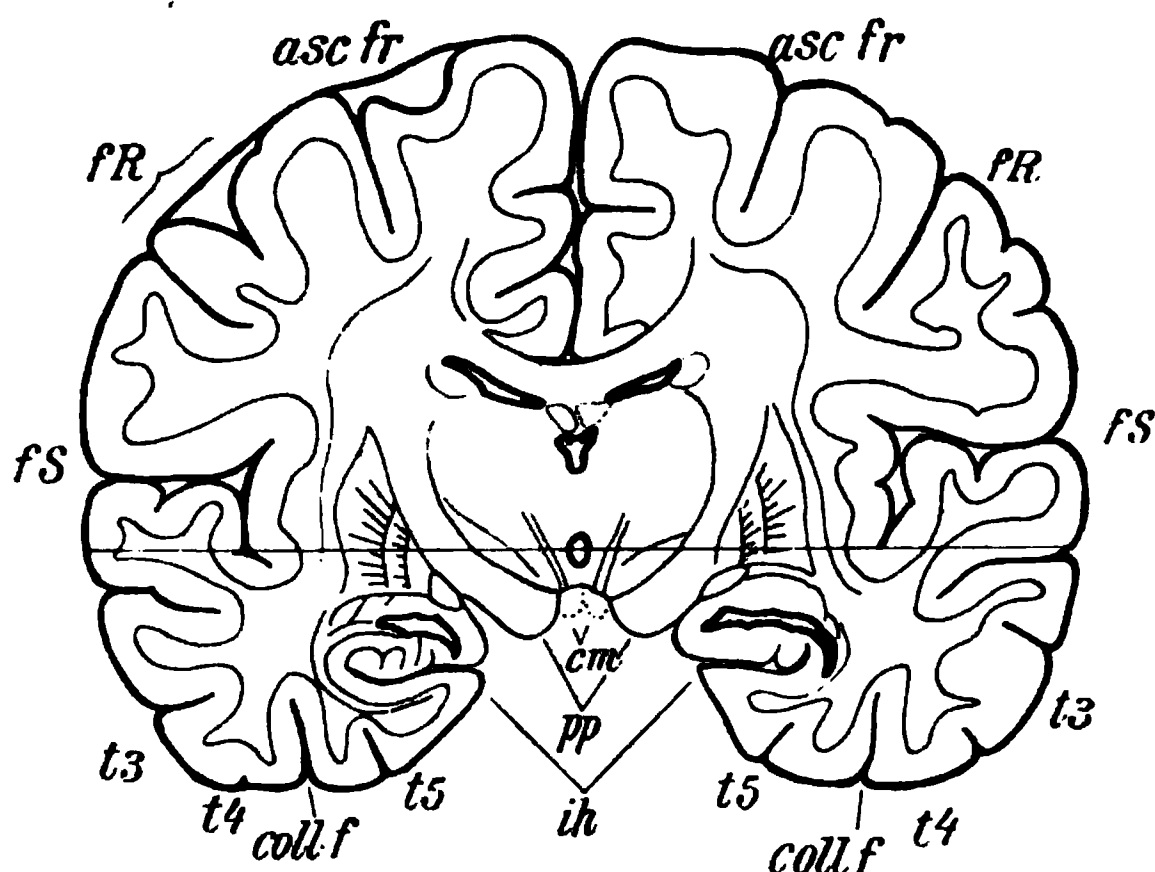


FIG. 6. —Frontal section of brain in the plane 6, figs. 1 to 3, passing through the middle commissure, and lying immediately behind the corpora mammillaria. The bodies of the lateral ventricles, which are of unequal breadth, lie beneath the corpus callosum, and upon the optic thalamus internally and the tail of the caudate nucleus externally. The inner border of the body of the lateral ventricle is in relation with the fornix and choroid plexus. The third ventricle is seen in two parts, lying respectively above and below the middle commissure; at its upper border its choroid plexuses are seen cut across. External to the optic thalamus lies the lenticular nucleus, the internal capsule intervening above and the pes pedunculi, *p.p.*, below. Still more externally is the island of Reil and posterior limb of the fissure of Sylvius. Below the lenticular nucleus is the curved extremity of the inferior horn of the lateral ventricle, *i.h.*, lying on the hippocampal gyrus, which is divided in the situation of the uncus. Between the hippocampal gyrus and the pes pedunculi the optic tract is seen on each side. The fissure of Rolando and the ascending frontal and collateral fissures are indicated in the figure, as are also the temporal convolutions.

The posterior cornua reach as far as the occipital lobes, without, however, appearing to extend any distance into these lobes,¹ their tips extending to within forty-five millimetres of the posterior extremity of the cerebrum (figs. 1 and 3). They

¹ The delimitation of the occipital lobes is not sufficiently precise to permit a more exact statement.

lie nearly thirteen millimetres behind the posterior end of the corpus callosum (right, eleven; left, fourteen millimetres).

The form of the lateral ventricles is not directly affected by the sulci seen on the surface of the hemispheres, except in the case

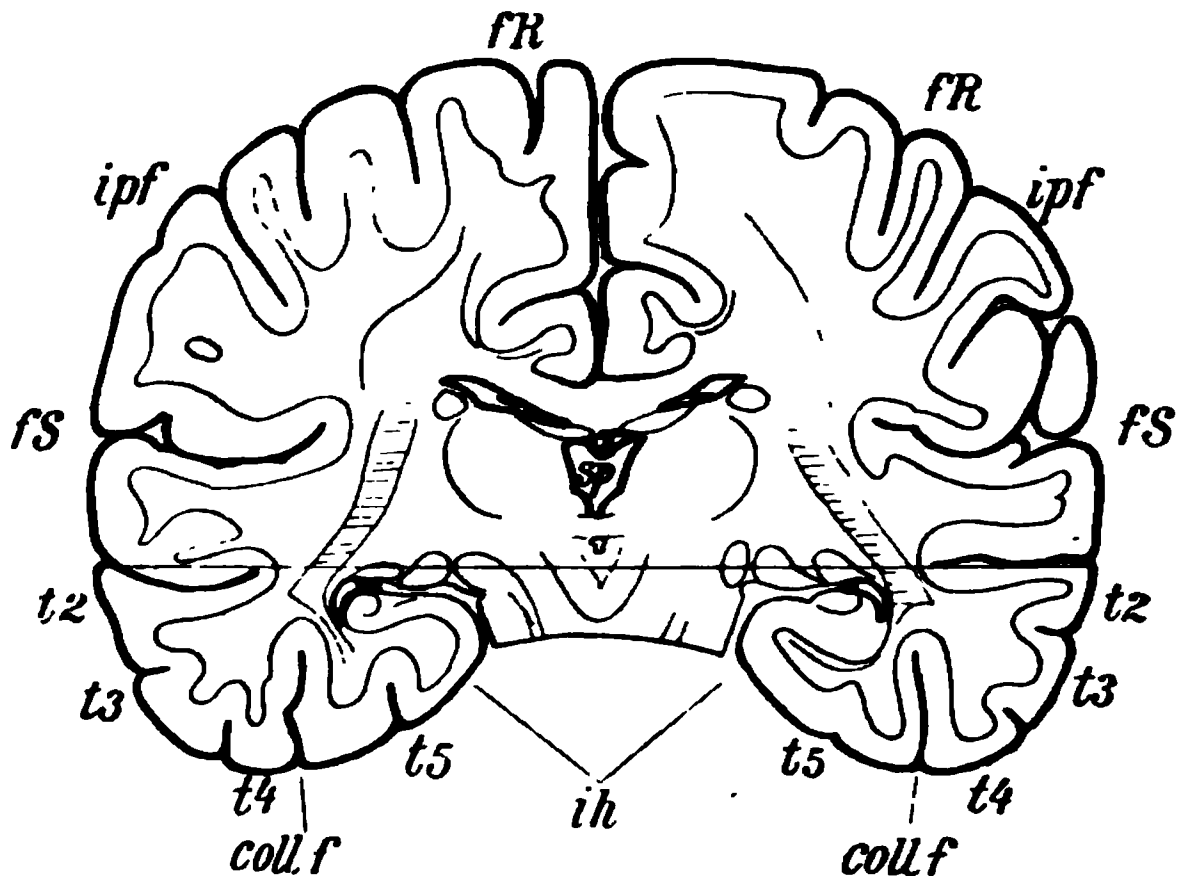


FIG. 7.—Frontal section of brain in the plane 7, figs. 1 to 3, passing through the posterior commissure. The bodies of the lateral ventricles are again seen lying beneath the corpus callosum, and resting below upon the lateral band of the fornix, the posterior portion of the optic thalamus [the choroid plexuses intervening] and the tail of the caudate nucleus. In the middle line below the corpus callosum is seen the supra-pineal recess, *s.r.*, of the third ventricle, above which the veins of Galen are seen cut across. Below the supra-pineal recess lies the posterior commissure, and beneath this again the upper end of the aqueduct of Sylvius [compare fig. 7 with figs. 2 and 10]. At the lower border of the section is seen in the middle line the tegmentum mesencephali, and on each side the pes pedunculi, the two being separated by the substantia nigra. On each side, lying above the hippocampal convolution, *t.5*, the descending horn of the lateral ventricle, *i.h.*, is seen. It lies above the hippocampus major and below the prolongation of the tail of the caudate nucleus [not shown in the figure]. At its inner border the choroid plexus of the descending horn is seen; externally it is in relation with the optic radiation and inferior longitudinal bundle. Lying above the optic thalamus are seen, proceeding from within outwards, the internal and external geniculate bodies and the optic tracts. The intra-parietal fissures are seen for the first time in this section.

of the dentate and collateral fissures, and the junction of the calcarine and internal parieto-occipital sulci, which correspond respectively to the hippocampal grooves on the inferior cornua, to the trigona ventriculi and collateral grooves, and to the hollow inner surfaces of the posterior cornua. The relation of

the lateral ventricles to the sulci seen on the vertex of the cerebrum is shown in fig. 3. The anterior extremities of the inferior cornua lie vertically below the precentral gyri, the outer limit of the posterior cornua corresponding approximately to a part of the intra-parietal sulci, and the tips of the anterior cornua lie vertically below the middle of the superior frontal convolutions.

The distance of the inferior horn from the body of the lateral ventricle (figs. 6 and 7; compare also figs. 10 to 14) is of

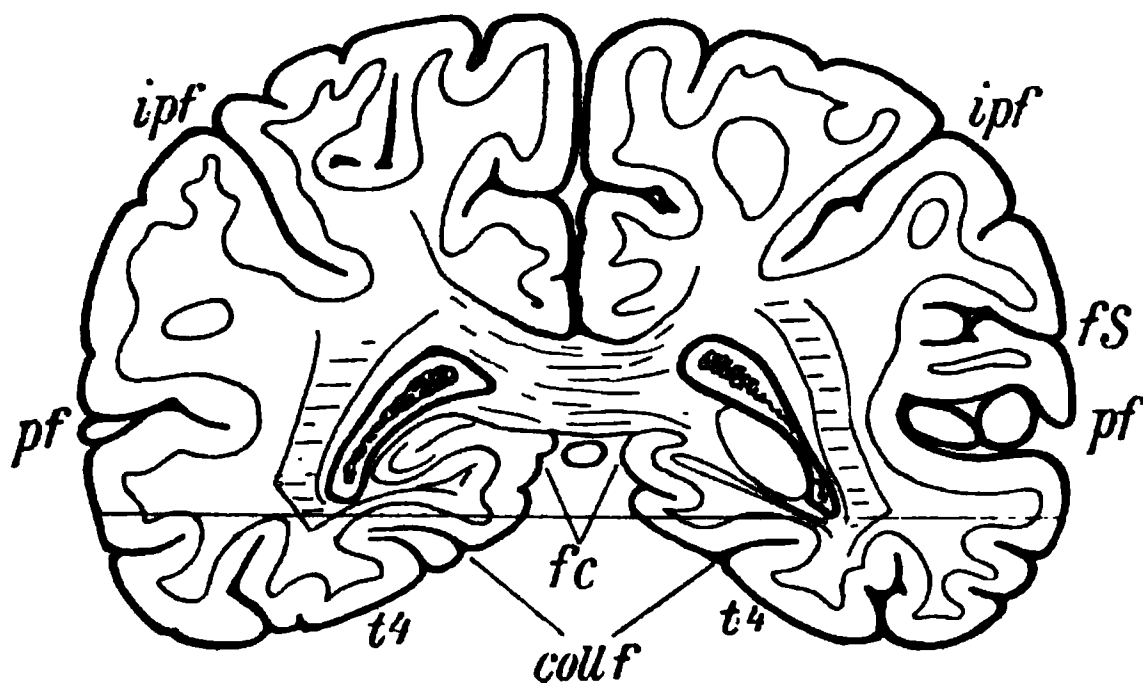


FIG. 8.—Frontal section of brain in plane 8, figs. 1 to 3, passing through the splenium of the corpus callosum and the posterior end of the pineal gland [which lies in the middle line immediately below the splenium]. The lateral ventricles are seen at the junction of body and inferior cornu. Within the lateral ventricles are the choroid plexuses. The outer surface of the ventricle is in relation with the optic radiation and inferior longitudinal bundle, and more externally with the posterior end of the first temporal and the adjoining convolutions [*p.f.* is the parallel fissure]. Internally the ventricle is here in relation with the posterior end of the hippocampus major and the forceps major of the splenium, *f.c.*, fasciola cinerea.

importance, since it is an index of the size of the basal ganglia, and is altered when atrophy of these structures occurs.

It now remains for the form of the various parts of the cerebral ventricular space, and their relation to the surrounding brain structures, to be considered in detail. We will commence with the third ventricle.

The third ventricle is a flattened, mesially placed space (fig. 10), roughly triangular in outline, and thus presenting two surfaces and three borders. It exhibits in about the middle of its extent a large opening, *m.c.*, corresponding to the middle

commissure (cp. fig. 6). In the model this opening is round, but it presents many variations of form, being sometimes elliptical, sometimes comma-shaped, and is not infrequently irregular in outline. The lateral surface of the third ventricle is bevelled off above and below, and presents a horizontal ridge lying in front of the middle commissure, commencing at the groove for the anterior commissure, and corresponding, approximately at any rate, to the junction of the optic thalamus above, and the olfactory and sub-thalamic regions below. The corresponding groove on the mesial surface of the thalam-

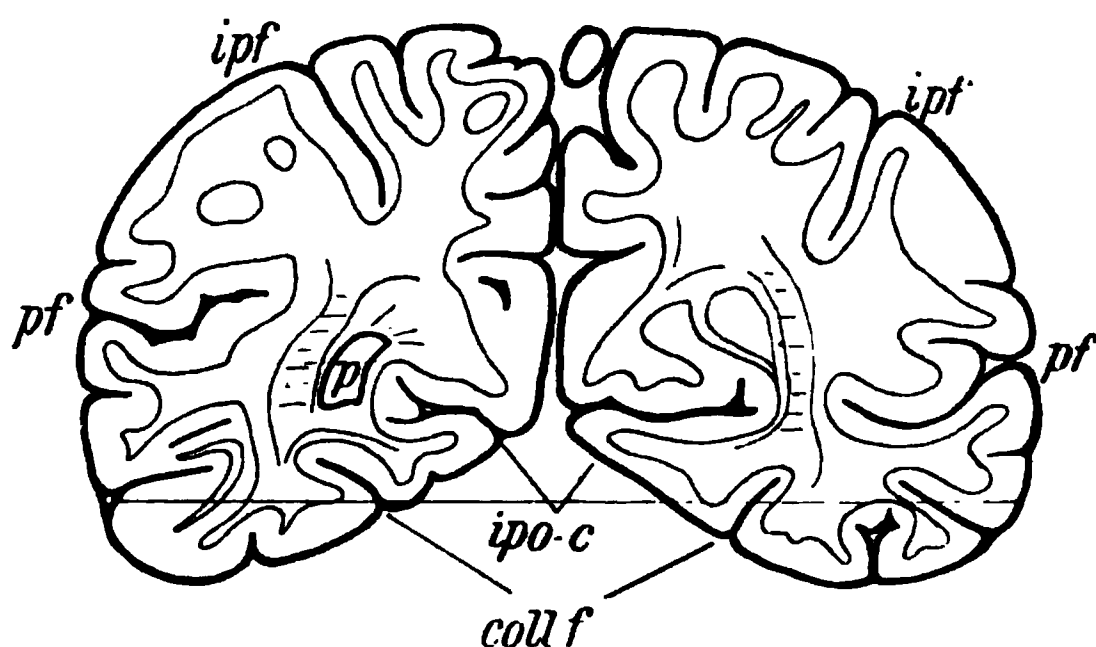


FIG. 9.—Frontal section of brain in the plane 9, figs. 1 to 3, passing behind the splenium of the corpus callosum and the tip of the right posterior cornu, and through the tip of the left posterior cornu. The latter is seen lying to the right of the left optic radiation and parallel fissure, *p.f.*, while its inner surface is opposite the common fissure, formed by the junction of the calcarine and internal parieto-occipital fissures, *i.p.o.-c.* The upper border of the tip of the left posterior horn is in contact with the forceps major of the corpus callosum, and the lower border approaches the bottom of the collateral fissure, *coll.f.*

encephalon is known as the sulcus of Monro. Behind the middle commissure, this ridge becomes less distinct. A slight groove running obliquely downwards and backwards on the lateral surface from the anterior superior angle of the third ventricle, lying behind the anterior commissure, *a.c.*, and becoming indistinct below, is generally recognisable. This, which is not well shown in the model, corresponds to the anterior pillar of the fornix. Nor does the model of the third ventricle show on its outer surface the fine curved groove, usually well seen in dissections of the brain, convex upwards, running from the

anterior superior angle, descending as it passes backwards to the pineal recess, and representing the stria pinealis.

The upper border of the third ventricle lies below the fornix (figs. 5 and 6). It is narrow from side to side, and presents, except at the posterior angle, two parallel fine grooves, corresponding to the choroid plexuses of this ventricle.

nc

h

p

FIG. 10.—The model of the cerebral ventricular cavity seen from the left side.

A comparison with the side elevation of the third and left lateral ventricles, given in fig. 2, will enable the reader to ascertain the position of the horizontal and vertical planes of figs. 2 to 9. The form of the third ventricle interrupted by the middle commissure, *m.c.*, and exhibiting complex anterior and inferior borders, should be compared with the mesial sagittal sections of the cerebrum given in works on anatomy. The expanded form of the supra-pineal recess, *s.r.*, is better appreciated by reference to figs. 1, 3, 12, 13. In noting the form of the anterior cornua and of the bodies of the lateral ventricles, this figure will require to be studied in association with the succeeding figures and the frontal sections given in figs. 4 to 9. The depression for the caudate nucleus, *n.c.*, is continued on to the inferior horn. The surface, *th.*, in relation with the fornix, choroid plexus, and optic thalam, is broad posteriorly where it lies internal to the groove for the caudate nucleus. [The narrower groove, corresponding to the choroid plexus of the lateral ventricle, which is especially well marked at the junction of body and posterior horn, is not shown in this and the three succeeding figures.] The inferior and posterior cornua, *i.h.* and *p.*, should be compared with the different positions shown in figs. 11, 12, and 13. This and the succeeding figures are of the natural size.

The anterior border is concave forwards, and presents at its middle the groove for the anterior commissure, above and below which it corresponds to the lamina terminalis. At the anterior inferior angle of the third ventricle is seen the deep notch for the optic chiasma, *o.r.* Above this is a projection representing the pre-optic recess.

The inferior border is straight or slightly concave downwards¹ in front, where it corresponds to the tuber cinereum, being prolonged into a projection, *i.*, indicating the infundibulum, and bounding the recess for the optic chiasma behind; more posteriorly, the inferior border becomes slightly concave downwards, corresponding in the middle line to the posterior perforated space and the tegmentum mesencephali. Still farther back is seen the upper opening of the aqueduct of Sylvius, *a.S.*, above which is the groove for the posterior commissure, *p.c.*, with a projection, *p.r.*, above it, forming the pineal recess. Still higher, and separated from the pineal recess by a concavity which may be somewhat broken in outline, is a large irregular prominence, *s.r.* (figs. 1, 3, 7, 10, 12, 13), the size and shape of which varies a good deal in different brains.

In studying the above points, the reader will derive considerable assistance from a comparison of figs. 2 and 10 with a mesial sagittal section of the brain.

At the anterior superior angle of the third ventricle is seen in the middle line a groove, continuous with the upper and anterior borders, on each side of which lies the rounded neck, flattened from side to side, by which the third ventricle becomes continuous with the lateral ventricle. The mesial groove is occupied by the pillars of the fornix and the lower edge of the septum lucidum, the former grooving the two divisions of the foramen of Monro on their inner and anterior aspect.

The anterior cornua, which are, as already stated, slightly unequal in size, the right being the larger, are flattened from side to side, and are separated in the middle line by an interval of two millimetres, corresponding to the septum lucidum (figs. 4, 11, 12, 13). The inner surfaces of the anterior cornua correspond very closely in form to that of the septum. Above, in front and below, each anterior horn presents a smooth bevelled surface, free from grooves, convex from side to side, corresponding to the genu and rostrum of the corpus callosum. The outer surface of each anterior cornu presents a large concavity, *n.c.* [figs. 10 to 13; cp. also fig. 4], for the head of the caudate nucleus. The edge of this concavity is sharp, and passes outwards much more above and in front than below and behind, in consequence of which

¹ This portion of the inferior border is sometimes slightly convex downwards.

the anterior cornua come to diverge from each other superiorly and anteriorly, while below and behind they approach each other more closely, as is indicated in the illustrations.

th

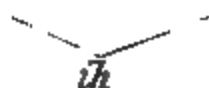


FIG. 11.—The model of the cerebral ventricular space seen from before. Note the flattened form of the third ventricle and the anterior cornua, and the incurving of the inferior cornua. Observe the surfaces for the caudate nuclei, *n.c.*, and optic thalami, *th*, and compare with the preceding figure and the frontal sections given in figs. 4 to 7. The depressions, *y.*, seen again in fig. 13, are described in the text. The left posterior horn, *p.*, is larger and longer than the right, its tip is directed outwards, while that of the right posterior cornu is turned slightly inwards, as the succeeding figure shows.

The bodies of the lateral ventricles are thicker anteriorly (fig. 5), and become more expanded as they pass backwards (figs 6, 7, 13). They are flattened from above downwards, and are placed obliquely, the inner border of each being at a lower level than the outer. The upper surfaces are flattened, and lie in immediate contact with the corpus callosum, the curvature of which they follow. The under surface consists of two parts: an outer part, *n.c.*, broader in front, narrow behind, corresponding to the tail of the caudate nucleus, and continuous posteriorly with the concavity on the inner surface of the anterior cornu; an inner part, *t.h.*, which is flattened and much broader than the other, especially behind. The latter presents a longitudinal irregular flattened groove (not shown in the figs.), more distinct posteriorly, which represents the choroid plexus of the lateral ventricle. On the outer side of this groove, the under surface

lies upon the *tænia semicircularis*; on the inner side it rests upon the corresponding lateral band of the fornix. The inner border lies farther outwards (figs. 5, 6, 7) on the left side than on the right. The inner borders of the bodies of the lateral ventricles, which are in contact with the fornix, approach each other anteriorly, where they come into relation with the choroid plexuses and the posterior extremity of the septum lucidum.

ac

trv

FIG. 12.—The model of the cerebral ventricular space seen from behind. Attention should be given to the form and relative position of the bodies and anterior and posterior cornua of the lateral ventricles, and also of the third ventricle which is seen on edge. On the inner aspect of each posterior cornu is the concave surface which comes in relation with the *forceps major* above and in front, the posterior end of the *hippocampus major* below and in front, and with the bottom of the common fissure formed by the junction of the calcarine and internal parieto-occipital sulci. The same surface is shown in the next figure; compare also figs. 8 and 9. The surface, *tr.v.*, represents the *trigonum ventriculi*, and corresponds to the collateral fissure. The impression of the *pes hippocampi* is seen on the under surface of the inferior cornua, *i.h.*, anteriorly, and should be compared with the section shown in fig. 6. Note also the large size of the *suprapineal recess*, *s.r.*

The general form and direction of the posterior cornua has already been described. They pass backwards and outwards, but in the case under consideration the tip of the right cornu is directed a little inwards, and that of the left somewhat more outwards (figs. 1 and 12).¹ Corresponding to this, the outer

¹ In several dilated ventricles that have come under my notice the incurving of the right posterior cornu has been marked, while the left has been less curved or has been slightly curved outwards.

surface of the right horn is convex, while that of the left is concave, from before backwards (fig. 10). Those surfaces come into close relation with the optic radiations and the inferior longitudinal bundles and posterior end of the claustrum (figs. 8 and 9). The inner surface of each posterior horn is marked by a deep concavity, *r.*, corresponding in front to the hippocampal convolution (fig. 8) and posteriorly to the common sulcus formed by the junction of the internal parieto-occipital and calcarine fissures (fig. 9), and coming into intimate relation with the forceps major of the corpus callosum, especially above and in front. The upper border of the posterior cornu, which is thick and rounded, is continuous with the inner border of the body of the corresponding lateral ventricle; the upper border and adjoining portion of the inner surface show several grooves caused by the forceps major (these are not reproduced in the illustrations). The inferior border of the posterior cornu is narrow behind, but is broader in front, at the junction of the posterior and inferior cornu, where it forms a triangular area representing the trigone (figs. 12 and 13); it corresponds to the collateral fissure, *coll.f.* (figs. 8 and 9).

The inferior cornu presents a slightly convex upper surface, which in front is separated from the lenticular nucleus by the inferior pedicle of the thalamus, while behind, where its position becomes more lateral, it comes into relation chiefly with the prolongation of the tail of the caudate nucleus (figs. 6 and 7). Its under surface is hollowed, and presents anteriorly four or five radiating grooves, broader in front than behind; these correspond to the pes hippocampi, while the rest of the under surface is occupied by the hippocampus major. The outer border is broad, and becomes continuous behind with the inferior border of the posterior cornu and the trigonal area; this border is in relation with the collateral fissure, and is separated from the upper surface by a thin edge (figs. 10 to 13). The inner border is thin, and stands in relation posteriorly to the choroid plexus of the descending horn (which lies above) and the posterior pillar of the fornix; both the latter structures stop short of the tip of the inferior cornu. At the junction of the body and descending horn of the lateral ventricle, the inferior surface of the inferior cornu is prolonged upwards, forming

a groove, which becomes narrower as it passes upwards, and is separated from the concavity on the inner surface of the posterior cornu of the lateral ventricle by a slightly curved border (figs. 11 and 13, *g*). Sometimes this groove, which is unusually well marked in the present case, merges gradually with the under surface of the body of the lateral ventricle, as



FIG. 13.—The model of the cerebral ventricular space seen from below. Most of the chief points which are here exhibited have been already referred to in the preceding figures, and need not be repeated. Note the mode in which the third ventricle becomes continuous on each side with the lateral ventricle at the junction of body and lateral horn, and compare with fig. 10.

is seen in the left lateral ventricle in figs. 11 and 13. It corresponds to the posterior end of the hippocampus major.

In conclusion, it may be again pointed out that the statements made in this memoir as to the form of the cerebral ventricular space have, except where otherwise stated, special reference only to the brain which formed the subject of

observation, and are not necessarily applicable to other brains without modification.

Addendum.—To the literature already given must be added a paper upon the topography of the lateral ventricles in respect of the cranium and the surface convolutions of the cerebrum, by E. A. Spitzka, *New York Medical Journal*, Feb. 2, 1901, based upon a study of two cases, and illustrated by projection drawings. This author gives the following additional references:—(1) Chipault, *Chirurgie opératoire du système nerveux*, tome i., 1894, fig. 153, reproduces from Poirier, *Topogr. cranio-encéph. et trépanation*, Paris, 1890, a side view of the skull with the ventricles outlined. (2) T. Stacey Wilson, three projection drawings of the brain, *Journ. of Anat. and Phys.*, vol. 28, 1894, pp. 228–235, studies the relation of the internal capsule to the surface convolutions of the cerebrum, and incidentally outlines the lateral ventricles. (3) Quain's *Elements of Anatomy*, Appendix, 1896, p. 8, gives a side view of the cranium, the lateral ventricles being indicated in outline.

Spitzka's drawings are very clearly made, and his paper will repay perusal. Wilson's figures are somewhat obscure. The outline in *Quain's Anatomy* is in illustration of cranio-cerebral topography.

EXPLANATION OF REFERENCE LETTERS.

- a.c.* anterior commissure.
- a.h.* anterior horn of lateral ventricle.
- a.p.s.* anterior perforated space.
- a.S.* aqueduct of Sylvius.
- asc.fr.* asc. frontal fissure.
- c.m.* corpora mammillaria.
- c.n.* concave depression for caudate nucleus.
- coll.f.* collateral fissure.
- f.c.* fasciola cinerea.
- f.R.* fissure of Rolando.
- f.S.* fissure of Sylvius.
- g.* vertical groove on inner surface of inferior cornu at its junction with the posterior cornu.
- i.* infundibulum.
- i.h.* inferior horn of lateral ventricle.

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- i.p.o.-c.* junction of internal parieto-occipital and calcarine fissures.
- l.* lateral ventricle.
- m.c.* middle commissure.
- n.c.* concave depression for caudate nucleus.
- o.r.* groove for optic chiasma.
- olf.tr.* olfactory tract.
- opt.tr.* optic tract.
- p.* posterior horn.
- p.c.* posterior commissure.
- p.f.* parallel fissure.
- p.h.* pes hippocampi.
- p.p.* pes pedunculi.
- p.r.* pineal recess.
- r.* concave inner surface of the posterior cornu.
- s.r.* supra-pineal recess.
- t.2, t.3, t.4, t.5.* 2nd, 3rd, 4th, 5th temporal convolutions.
- th.* under surface of lateral ventricle, in relation to the optic thalamus.
- t.l.* temporal lobe.
- tr.v.* trigonum ventriculi.
- 3. third ventricle.



FIG. 14.—Perspective representation of model seen from before and a little to the left. This sketch, taken in conjunction with figs. 10 to 13, will give a clearer general idea of the relations of the bodies and cornua of the lateral ventricles to each other and to the third ventricle than the other sketches, which, however, furnish further and more precise information on matters of detail. The asymmetry of the posterior cornua is recognisable, but not that of the bodies of the lateral ventricles. The form of the posterior and inferior cornua and of the third ventricle should be compared with that shown in the models of Welcker, Testut, and Retzius.

THE PERITONEUM OF THE PELVIC CAVITY. By
A. FRANCIS DIXON, M.B., Sc.D., *Professor of Anatomy,
University College, Cardiff*, and AMBROSE BIRMINGHAM, M.D.,
Professor of Anatomy, Catholic University, Dublin. (PLATES
V.—VII.)

WHEN bodies are hardened by the intravascular injection of strong solutions of formalin, the ureter, vas deferens, bladder, and other pelvic structures, muscular and fibrous, become firm, indeed almost rigid, and many of them are seen to give rise to projections or ridges of the peritoneum, which are more easily studied than in the ordinary unhardened condition. The peritoneum itself, too, becomes fixed; and many details of its arrangement, which are often obscure in soft bodies, become comparatively clear.

In such a body, with the bladder and rectum empty, the peritoneum lining the pelvic cavity is arranged in the form of three great primary fossæ—an anterior, related to the bladder, a posterior, related to the rectum, and a middle, related to the uterus in the female, to the vasa deferentia and the vesiculæ seminales in the male. The term 'fossa' is suggested for these subdivisions of the pelvic cavity for want of a better name, and is not used in the strictest sense of the word. These three pelvic fossæ might be compared to the great fossæ of the base of the cranium, to which, indeed, in a general way, they bear a slight superficial resemblance.

THE ANTERIOR PRIMARY FOSSA OF THE PELVIC PERITONEUM corresponds to what may be called the vesical region of the pelvic cavity. The bladder, when empty, lies in its central portion; when distended, it occupies almost the entire fossa.

This fossa is separated from the middle primary fossa behind by the line of the ureters, which latter, together with the surrounding tissue and vessels, except when a considerable

amount of subserous fat is present, may be seen shining through the peritoneum, or may even produce two fairly distinct ridges running downwards and inwards to reach the lateral angles of the bladder. Between the terminations of the two ureters the fossa is limited by the posterior border of the bladder, the position of which is always easily identified in the empty condition.

In front and at the sides, the fossa extends up to the pelvic brim, and further back, just in front of the ureter, to the level of the external iliac vein. The fossa is made up of two large lateral concave portions, triangular in shape, separated from one another by the projection of the empty bladder, and of a mesial convex part corresponding to the upper surface of the bladder itself. The *middle subdivision* of the anterior primary fossa requires no special description. It is triangular in outline, corresponds in extent to the upper surface of the bladder, and it is sometimes crossed by the peritoneal fold, or folds constituting the *plica vesicalis transversa*.

The Lateral Subdivisions of the Anterior Primary Fossa which lie at the sides of the bladder approach each other in front at the bladder apex, where they are merely separated by the urachus. They are limited—*below* (or internally), by the lateral border of the bladder and proximal part of the urachus; *behind*, by the ureter, which produces a distinct, though slight, ridge of the peritoneum when the bladder is firmly contracted; and *above and in front* (*i.e.* laterally), by the brim of the pelvis, and also in part by the external iliac vessels near their origin. The lower part of the peritoneal ridge or fold which indicates the course of the ureter usually contains also the inferior vesical and middle hæmorrhoidal vessels; the fold is usually more distinct in its lower than its upper part.

Beneath the peritoneum of this district of the pelvic wall are found the body and superior ramus of the pubes anteriorly, and the obturator internus muscles more posteriorly.

Each lateral subdivision of the fossa is crossed from before backwards by the horizontal portion of the vas deferens, which can usually be seen shining through the peritoneum as it runs backwards in a somewhat wavy course on the pelvic wall. A

triangle is thus marked off above the vas, which is approximately equilateral—the sides measuring about two inches (one and a half to two and a quarter inches). This practically corresponds to Waldeyer's *fossa obturatoria*, and is bounded by the ureter behind, by the vas deferens below, and by the external iliac vein and pelvic brim above and in front. Below the fossa obturatoria, and separated from it by the vas deferens, is the *para-vesical fossa* of Waldeyer. This fossa is somewhat quadrilateral in outline, and is bounded in front by the pelvic brim, behind by the ureter, above by the vas, and below by the lateral border of the bladder and the proximal part of the urachus. The fossa obturatoria and the para-vesical fossa, as here described, taken together, constitute the lateral subdivision of the anterior fossa of the pelvis as defined above. (See Plate VI.)

It must be noticed that the obturator and para-vesical fossæ just described do not exactly correspond to the districts to which Waldeyer,¹ in his work upon the topographical anatomy of the pelvis, has given these names. Waldeyer's obturator fossa is limited above by the obliterated hypogastric artery (arteria umbilicalis), and therefore does not extend upwards to quite so high a level as the district to which we have ventured to apply the same name. In fact, the fossa as described by him does not quite reach the pelvic brim. In the case of the para-vesical fossa, Waldeyer includes within it the deep epigastric artery (vasa epigastrica inferior), and thus this fossa, as described by him, lies partly above the pelvic brim. We believe that it will be found more convenient to restrict the term 'para-vesical fossa' to the district which lies below the brim of the true pelvis. The portion above is usually distinctly marked off, and belongs to the abdominal cavity proper. The description which we have given corresponds more accurately with that given by Waldeyer at a meeting of the Anatomical Society held in Dublin in June 1897.²

The obliterated hypogastric artery forms a slight (sometimes a prominent) ridge as it runs downwards and forwards on the

¹ " *Das Becken*," 1899, p. 238.

² "Topographical Sketch of the Lateral Wall of the Pelvic Cavity," *Jour. of Anat. and Phys.*, xxxii., 1897, p. 1.

pelvic wall, close to the brim of the pelvis, which it finally crosses obliquely in its course to reach the anterior abdominal wall. Having traversed the obturator fossa, the hypogastric vessel almost always crosses the upper anterior angle of the para-vesical fossa before it leaves the pelvis. When fat is absent, the obturator vessels and nerve may be seen running forwards and downwards beneath the peritoneum of the obturator and upper part of the para-vesical fossa, and lying at a lower level than the hypogastric artery.¹ Under similar conditions, the vesical vessels can be distinguished as they run inwards across the fossæ to reach the bladder. (Plate VI.)

The para-vesical fossa is also crossed by the variably developed *plica vesicalis transversa* (Waldeyer), a small fold of peritoneum which runs outwards from the upper surface of the empty bladder across the pelvic floor to the side of the pelvis, and generally pursues a course in the direction of the internal abdominal ring. In size, the fold is very variable—sometimes extremely small, it extends out but a short distance from the bladder; in other cases, and commonly in the foetus, it can be traced across the pelvic brim as far as the internal abdominal ring. It may or may not join with its fellow on the upper surface of the bladder. Sometimes several folds are present, while occasionally no representation of the plica can be distinguished, or the fold may be present upon one side and absent on the other. On the whole, the plica transversa seems to be better developed and more constantly present in the male than in the female, a fact which is probably to be associated with the greater development of the processus vaginalis in the male foetus.² The fold often corresponds in position on one or both sides to the course of the superior vesical artery. We have found the fold too variable, both in occurrence and position, to serve as a practical or useful line of subdivision of the para-vesical fossa into anterior and posterior portions as described by Waldeyer.³

¹ The exact relationships of these structures has been described by Waldeyer, "*Das Becken*," and *Jour. of Anat. and Phys.*, loc. cit.

² Compare A. F. D., "The Form of the Empty Bladder and its Connections with the Peritoneum," *Jour. of Anat. and Phys.*, vol. xxxiv., Jan. 1900, p. 193.

³ "*Das Becken*," page 238, and *Jour. of Anat. and Phys.*, vol. xxxii., 1897, page 1.

In front, the peritoneum of the anterior pelvic fossa is continued upwards, across the pelvic brim, into that of the inner and middle inguinal pouches or fossæ (fovea supravescalis and fovea inguinalis medialis). Near the middle line the transition of the pelvic peritoneum into that of the anterior abdominal wall is direct at the pelvic brim; farther from the middle line, however, the peritoneum is at first continued across a triangular interval, and forms a little fossa before it reaches the abdominal wall from the pelvis. This little interval or fossa, which we have called the *trigonum femorale*, may be considered to be formed in the following manner:—the external iliac vein pursuing a direct course downwards and outwards to pass beneath Poupart's ligament, leaves the pelvic brim about one and a half to two inches in front of the point where the ureter enters the pelvis; in this position the ilio-pectineal line arches inwards and downwards, and thus an angular interval is left between these two structures. This interval, which is a portion of the abdominal, and not of the pelvic cavity, is the *trigonum femorale*. It is bounded externally by the external iliac vein, internally by the lower part of the ilio-pectineal line, and anteriorly and below by the inner part of Poupart's ligament. Beneath the peritoneum lining the fossa is the origin of the pectineus muscle, and usually some lymphatic glands of the iliac group. At the lower and outer part of the triangle is the *fovea femoralis*, or depression corresponding to the position of the crural ring. The upper angle of the triangle, which lies between the ilio-pectineal line and the iliac vein, is very acute, and is crossed by the abdominal part of the vas deferens, here passing backwards from the internal abdominal ring to enter the pelvis. The lower and inner part is crossed by the fold of peritoneum (*plica umbilicalis lateralis*), which contains the obliterated hypogastric artery, as it turns upwards from the pelvis to reach the anterior abdominal wall. This fold is very variable; not infrequently it is strongly marked, and may project in its lower part from a half to one inch into the abdominal cavity, giving the fovea femoralis, which lies to its outer side, the appearance of a deep pyramidal fossa opening upwards into the abdominal cavity. The lateral portion of the *plica vesicalis transversa*, in those cases in which that fold is strongly

developed, is also found on the floor of this fossa as it is continued outwards towards the internal abdominal ring. (Plates V. and VI.)

The term 'excavatio-parietovesicalis' is used by Waldeyer to indicate the groove-like depression at the bottom of which the peritoneum of the side wall of the pelvis and that covering the bladder become continuous. When traced backwards, this peritoneal groove is described as running into the recto-vesical pouch, the line of separation of the two depressions being, however, marked by the 'recto-vesical' fold. The outer wall of this groove, in as far as it lies in front of the fold formed by the ureter, is a portion of the para-vesical fossa. We do not consider the term 'excavatio-parietovesicalis' applicable to any part of the peritoneum which lies behind the lower end of the ureter and posterior border of the bladder, and we would suggest that the term, if it is to be used at all, be restricted to the part of the groove which lies in front of the plane determined by these structures. The district behind the ureter and in front of the 'recto-vesical' fold is a portion of the middle primary fossa or genital subdivision of the pelvic cavity as described by us. In the female, the central portion of this district is occupied by the uterus, and the more lateral part forms the fovea para-uterina (Waldeyer); in the male, the terminal parts of the vasa deferentia and the seminal vesicles occupy a corresponding position. (See Plates.)

THE POSTERIOR PRIMARY FOSSA OF THE PELVIC PERITONEUM forms what may be termed the rectal subdivision of the pelvic cavity, since the empty rectum occupies its central portion—the distended organ the greater part of the fossa.

This large fossa is limited by the posterior wall of the pelvis behind, and is separated from the middle fossa in front when the bladder is empty by a prominent crescentic fold (sacro-genital fold) which runs across transversely, about a half to one inch behind the posterior border of the bladder. Laterally, this fold curving backwards fades away into the peritoneum on the side wall of the pelvic cavity, and beyond this the middle and posterior primary fossæ are confluent in the hypogastric fossa (of Waldeyer). In front of the free projecting edge of the fold

just mentioned the vas deferens turns inwards towards the base of the bladder. (See Plates V. and VI.)

The anterior wall of the posterior fossa, which is overhung by the crescentic fold, is nearly vertical, and corresponds chiefly to the posterior aspects of the ampullary portions of the vasa deferentia near the middle line, and to the seminal vesicles more laterally. In the female it is formed by the cervix uteri and the upper part of the vaginal wall. The height of this wall varies, according to the conditions of the bladder and rectum, from one-eighth to three-quarters of an inch in the male, but it is usually greater—three-fourths to one inch—in the female. It is also nearly always greater laterally than in the middle line of the pelvis, corresponding to the greater depth of the posterior fossa in this position.

The projection of the empty rectum divides the posterior primary fossa into two lateral concave portions, already described by one of us¹ as the para-rectal fossæ. These correspond in their nature to the para-vesical fossæ described above, and their relationship to the rectum is comparable to that of the latter fossæ to the bladder. When the two organs are empty and contracted, the laterally placed fossæ are large and distinct, but as the bladder and rectum become distended, the fossæ become smaller or almost obliterated, owing to the enlarged organs invading the fossæ and stripping the peritoneum off the adjacent portion of the pelvic wall. The reduction of the fossæ is, however, much more complete in the case of the para-vesical than in the case of the para-rectal fossa.

Where the rectum turns down to pierce the pelvic floor the pararectal fossæ of opposite sides may be said to meet in the middle line inferiorly, at the bottom of the little peritoneal depression which lies below the level of the crescentic fold, and between the rectum behind and the vasa deferentia (or upper part of vagina in the female) in front. This depression as seen in mesial section is known as the recto-vesical pouch, or pouch of Douglas. The term *recto-genital* has been suggested by one of us as being more accurate than recto-vesical in the case of the

¹ A. B., "Some Points in the Anatomy of the Digestive System," *Jour. of Anat. and Phys.*, vol. xxxv., Oct. 1900, p. 65.

male, and as being appropriate also to the corresponding depression in the female.¹ When traced upwards from this point, where they are confluent, the para-rectal fossæ are at first separated from one another by the width of the rectum; higher up, however, above the third sacral vertebra, the pelvic mesocolon alone intervenes between the fossæ of opposite sides. On the left side the upper limit of the para-rectal fossa lies at the point where the pelvic mesocolon crosses the iliac vessels; on the right the fossa ends superiorly at a line drawn outwards from the sacral promontory to meet the iliac vessels. It is the lower portions of the fossæ which become taken up and obliterated during distension of the rectum. The peritoneum forming the para-rectal fossa lies in front of the lateral part of the sacrum and the pyriformis muscle. Beneath it are also to be found the anterior divisions of the sacral nerves, with some of their branches and connections, the pelvic portion of the sympathetic cord, the lateral sacral vessels, and on the right side a portion of the middle sacral artery. On the left side branches of the superior hæmorrhoidal vessels are present. Beyond the lateral margin of the sacrum the peritoneum of the side wall of the pelvis sweeps forwards, covering the large branches of the internal iliac artery, and the para-rectal becomes continuous with the hypogastric fossa. In the undissected part, no ridge or mark can be made out which will give a suitable boundary between these two peritoneal-covered districts of the pelvic wall. Waldeyer² describes the lateral border of the sacrum as forming the limit of the hypogastric fossa, yet he notices that the 'recessus para-rectalis'—a chink which intervenes between the rectum and side wall of the pelvis—may have branches of the iliac artery, or even the ureter, in its outer wall when the rectum is distended. Thus the outer wall of Waldeyer's 'para-rectal recess,' which corresponds in part to the para-rectal fossa described in this paper, may, in the

¹ A. F. D., *loc. cit.*, page 192. B. Cuneo and V. Veau ["Signification morphologique des Aponévroses périvésicales," *Journal de l'Anatomie*, 1899, page 244] use the term 'sémino-rectal.' Fredit [*Traité d'Anatomie humaine* (Poirier), Tome iv., 1900, page 1042] describes the pouch as 'recto-séminale' in the male, and emphasises the fact that the pouch is 'vésiculo-rectal' rather than 'recto-vesical.' He uses the term 'cul-de-sac génito-rectal' for both sexes.

² *Loc. cit.*, page 240 and page 271.

distended condition of the rectum, include the hypogastric fossa. The same recess has been described by Jonnesco under the name 'fosse recto-pelvienne.'¹

THE MIDDLE PRIMARY FOSSA OF THE PELVIC PERITONEUM.—As the anterior fossa is related to the bladder and the posterior fossa to the rectum, similarly the middle fossa is related to the terminal portions of the genital ducts of the embryo, to the vasa deferentia and vesiculæ seminales in the male, and the uterus in the female adult.

This middle fossa, which is narrow mesially, but wider laterally, is separated from the anterior fossa by the ureter and the posterior border of the empty bladder. Posteriorly it is limited in the male by the crescentic (sacrogenital) fold which runs transversely one-half to one inch behind the posterior border of the empty bladder. In the female the separation of the middle from the posterior primary fossa is effected by a similar crescentic fold, the lateral parts of which are the folds of Douglas (plicæ recto-uterinæ). These latter are continuous across the middle line at the back of the uterus, in the vicinity of the isthmus, and constitute there a slight ridge known as the torus uterinus. (See Plates VI. and VII.)

Above (*i.e.* laterally), the fossa broadens out, and passes without demarcation into the side wall of the posterior part of the pelvis. The portion of the vas deferens which passes backwards beyond the ureter marks off in the male an upper lateral from a lower mesial subdivision of the middle primary fossa, the former appearing on the side wall, the latter on the floor of the pelvic cavity. The lateral subdivision is the more extensive, and corresponds in part to the fossa hypogastrica of Waldeyer. It is not marked off posteriorly from the upper lateral part of the para-rectal fossa. Beneath the peritoneum of this part of the side wall of the pelvis lie several of the branches of distribution of the internal iliac (German, hypogastric) vessels. (See Plates V. and VI.)

The mesial subdivision is narrow, and is continuous with the corresponding district across the middle line, forming a horizontal shelf which runs transversely behind the (empty)

¹ *Traité d'Anatomie humaine* (Poirier), Tome iv., 1895, p. 358.

bladder. Immediately beneath the peritoneum of this shelf lie the upper ends of the seminal vesicles and the transverse portions of the vasa deferentia. The bladder during distension invades this part of the pelvis, and the peritoneum is then taken up in such a manner that the mesial subdivision of the middle fossa practically disappears. Near the middle line, just behind the empty bladder and between it and the vasa deferentia, here, approaching one another, is often found a slight depression, which we believe corresponds to the utero-vesical pouch of the female. The term 'genito-vesical' pouch or depression seems applicable to this recess in both sexes.¹

In the female the peritoneum of the central part of the middle primary subdivision of the pelvic cavity is raised up to cover the body of the uterus, as low down as the isthmus. Below the level of the torus uterinus, the peritoneal covering of the uterus is derived from the recto-genital pouch—a portion of the posterior primary subdivision of the pelvic peritoneum. At each side of the uterus, between the crescentic (sacro-genital) fold behind and the ridge produced by the ureter in front, is a distinct fossa or depression, named by Waldeyer the fovea para-uterina. The outer wall of this depression is formed by the side wall of the pelvis, and becomes continuous with the hypogastric fossa.

Behind the plane determined by the ureter a variably developed but often strongly marked ridge may be seen in both sexes, passing nearly vertically downwards on the side wall of the pelvis. This ridge, somewhat variable in position, often meets the line indicating the course of the ureter near the point where the latter is crossed by the vas deferens in the male. When traced upwards, it passes in the direction of the sacral

¹ The presence of this depression in the adult and its significance has already been noted by one of us. (A. F. D., *loc. cit.*, p. 190.) The earlier recorded and interesting observations of Cunéo and Veau (*loc. cit.*, p. 242) have demonstrated that the fossa in question is strongly marked in the embryo, and that during the course of development there is a complete correspondence in the arrangement of the peritoneum of this region in the two sexes. They apply the term 'cul-de-sac vésico-seminal' to this fossa in the male embryo, and to the corresponding fossa when it persists in the adult. See also Fredit (*loc. cit.*, p. 1042), who uses the terms 'cul-de-sac vésico-seminal' and 'cul-de-sac génito-vésical' for this depression in the embryo and in the child.

promontory. Beneath the peritoneum of the ridge is to be found the nerve cord which connects the upper part of the hypogastric plexus (interiliac plexus) with the pelvic plexus. In some cases the ridge is double on one or both sides. We are inclined to believe that these peritoneal ridges or folds are the 'ligaments utéro-lombaires' described by Vallin,¹ or 'plicæ utero-lumbales' of Waldeyer.² Each nerve cord, with its surrounding connective tissue, is closely adherent to the front of the last lumbar and first sacral vertebræ superiorly, and below joins the great ganglionic mass situated near the outer end of the seminal vesicles or at the side of the cervix uteri. They might easily be mistaken for tissue similar to that enclosed within the folds of Douglas in the female. Although we are not in a position to state that in every case these ridges or folds are produced by nerve cords, still we believe that in a majority of instances they will be found to be so produced. The ridges which we have found to be produced in the manner mentioned agree exactly in position with the 'ligaments utéro-lombaires' as described by Vallin. (See Plates VI. and VII.)

The crescentic fold, which separates, in the manner described above, the middle from the posterior primary fossa of the pelvic peritoneum, requires further notice. In the female it is composed of two lateral portions, the folds of Douglas or plicæ recto-uterinæ, and of a mesially placed connecting portion, the torus uterinus. In the male the fold is always distinct when the bladder is empty and contracted. Its free edge, especially well marked near the mesial plane, projects horizontally backwards and overhangs the recto-genital pouch. This edge lies some distance, one-eighth to half an inch, behind the plane of the vasa deferentia as they turn inwards. As the bladder becomes distended, the mesial portion of the fold becomes taken up, but we have found the lateral portions well marked in a male subject in which the bladder was normally distended, and contained just ten ounces of fluid. Microscopic examination shows that the fold in the male, as in the female, contains a considerable number of smooth muscular fibres, and that these

¹ "*Situation et Prolapsus des Ovaires*," Paris, 1887, pp. 14-17, and plates i. and ii.

² *Loc. cit.*, pp. 495, 531, and 533, and figs. 81a and 85, pp. 439 and 462.

are present even near the free edge of the mesial part, where the two layers of peritoneum composing the fold are almost in apposition. This muscular tissue becomes continuous with that which is often present in considerable quantity surrounding the seminal vesicles and terminal portions of the vasa deferentia. When traced into the lateral part of the fold, the muscular tissue seems to become connected with the tissue on the posterior aspect of the rectum and with that on the front of the sacrum. Here, however, it is difficult to make out definite connections. Numerous minute blood-vessels running transversely can often be recognised by the unaided eye in this fold. These are probably the vessels which have been described in the female as establishing communications between the vessels of the rectum and those of the vagina and uterus. We have found these vessels present in the male, even in the middle line, and close to the free edge of the fold. Since there is so close an agreement in these folds in the two sexes, we consider that it is suitable to apply the same name in each case, and to speak of sacro-genital folds, or folds of Douglas, both in the male and in the female. The contained fibrous and muscular tissue will constitute in both sexes the sacro-genital ligaments and the recto-genital muscles respectively. In the specimens which we have examined, it was not possible, however, to distinguish between these ligaments and muscles, but a continuous mass of mixed fibrous and smooth muscular tissue lay within the fold.

With regard to the relations presented by the round and broad ligaments of the uterus to the fossæ described in this paper, we have merely the following notes to add. The round ligament forms in the female the lower boundary of the obturator fossa, and separates it from the para-vesical fossa. It is not by any means so intimately related to the ureter as the vas deferens is in the male. The round ligament leaves the side wall of the pelvis to enter the broad ligament when in its course it has reached the plane of the ureter, or sometimes even before it has passed so far backwards. In the latter case the obturator and para-vesical fossæ are incompletely separated in their posterior parts. The attachment of the broad ligament to the pelvic wall descends almost vertically through the obturator and through the extreme posterior part of the para-vesical fossa. In

its lowest part the attachment of the ligament to the floor of the pelvis lies just over or immediately behind the terminal part of the ureter. The ovary lies in the posterior part of the obturator fossa, which is divided into anterior and posterior portions by the line of attachment of the broad ligament. We have nothing to add to Waldeyer's graphic and accurate descriptions of the fossa ovarica, and of the relations which it presents to the ureter and other neighbouring structures.

CONCLUSIONS.

The following brief account of the pelvic peritoneum gives the chief conclusions at which we have arrived. As will have been seen, many of them are in close agreement with Waldeyer's results.

I. In the hardened body, with empty bladder and rectum, the peritoneum of the pelvis forms one general cavity, practically coextensive with the pelvic cavity itself. This is subdivided by more or less distinct ridges of peritoneum—caused by the projection of underlying structures—into *three primary districts or fossæ*, which are morphologically equivalent in the two sexes, namely, an anterior or vesical, a middle or genital, and a posterior or rectal.

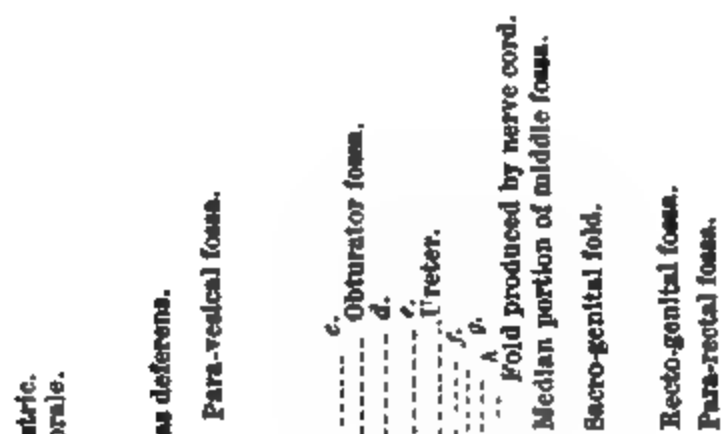
II. *The anterior primary fossa* is separated from the middle at each side by a slight peritoneal ridge, corresponding in position to the ureter, coursing downwards and inwards to the lateral angle of the bladder, and between these by the posterior border of the bladder. It presents in its middle region a convex triangular area corresponding to the upper surface of the bladder. On each side of this is an elongated depression, extending from the lateral border of the bladder internally to the horizontal portion of the vas deferens laterally, and known as the *para-vesical fossa*, which is invaded by the bladder on distension, and thus reduced to a mere slit or fissure. Still further out on the side wall of the pelvis and above the vas deferens is the *fossa obturatoria*, which is bounded in front by the external iliac vein and behind by the ureter. In the posterior part of the fossa obturatoria is situated the *fossa ovarica* of the female.

III. *The posterior primary fossa* is separated from the middle fossa by two well marked peritoneal ridges—the two *sacro-genital folds*—which are produced by the sacro-genital ligaments. These are two bands of mixed fibrous and muscular tissue which pass from the region of the genital ducts in the male (of the isthmus uteri in the female) outwards and backwards on each side, to blend with the tissue on front of the lower end of the sacrum and the back of the rectum. The two sacro-genital folds become continuous with one another about half to one inch behind the bladder in the male; on the back of the isthmus uteri, forming the torus uterinus, in the female.

The posterior primary fossa presents a central area corresponding to the rectum, at each side of which is an elongated depression—the *para-rectal fossa*. This latter is invaded by the rectum during distension. Inferiorly, as the rectum sinks down to pierce the pelvic floor, the two para-rectal fossæ become continuous in front, and this lower part of the posterior primary fossa is known in the female as Douglas's pouch; it may be called in both sexes the *recto-genital pouch* or fossa, for it lies between the rectum behind and the genital ducts—vasa deferentia and seminal vesicles, or cervix uteri—in front.

Laterally, above the level of the sacro-genital folds, the para-rectal fossæ pass without demarcation into the hypogastric fossæ on the side wall of the pelvis.

IV. *The middle primary fossa*, which is related to the terminal portions of the genital ducts—the vasa deferentia and seminal vesicles in the male, and the uterus in the female—is separated, as already described, from the anterior fossa by the ureters at the sides, and by the posterior border of the bladder mesially. The sacro-genital folds separate it from the posterior fossa. In the male it is divided by the portion of the vas deferens which lies behind the plane of the ureter into a wider lateral part, which passes into the hypogastric fossa on the side of the pelvis, and a narrower shelf-like mesial part, beneath which lie the seminal vesicles and the transverse portions of the vasa deferentia. The bladder during distension invades this mesial part, which may then be said to disappear. There is often present, between the bladder in front and the ends of the vasa deferentia behind a slight depression—well marked in the embryo—which corre-



Cast of a mesial section of the male pelvis. The cast was exhibited at a meeting of the Anatomical Society, May 1901.—A. F. D.

The dark broken line indicates the position of the lower part of the ilio-pectineal line—the inner boundary of the trigonum femorale. *a*, plica vesicalis transversa; *b*, vesical arteries; *c*, obturator artery; *d*, vesical artery; *e*, hæmorrhoidal artery; *f*, gluteal artery; *g*, internal pudic artery; *h*, sciatic artery.

PROF. DIXON AND PROF. BIRMINGHAM.

l.
foam.
r fossa (anterior subdivision).
in vessels.
rior fossa (posterior subdivision).
r.
produced by nerve cords.
rectal fossa.

Recto-genital fossa. Sacro-genital fold.

Cast of a mesial section of the female pelvis, prepared from a dissection of Dr E. H. Taylor's. The cast was exhibited at a meeting of the Anatomical Society, May 1901.—A. F. D.

The dark broken line indicates the position of the lower part of the ilio-pectineal line—the inner boundary of the trigonum femorale.

PROF. DIXON AND PROF. BIRMINGHAM.

sponds to the utero-vesical pouch of the female. The term *genito-vesical pouch* may be applied to these corresponding parts in both sexes.

In the female the uterus projects upwards in the mesial portion of the middle fossa; at each side of it is a depression, the *fovea para-uterina*, which passes without demarcation into the lateral portion of the middle fossa.

V. The line of attachment of the broad ligament runs from the side of the uterus, out over the terminal part of the ureter, then upwards across the extreme posterior portion of the para-vesical fossa to enter the obturator fossa. As it traverses the latter it marks off a posterior part, the *fossa ovarica*, in which the ovary lies.

VI. In the female the round ligament separates the para-vesical from the obturator fossa.

VII. On each side, behind the ureter, a ridge may often be seen passing downwards and inwards. These have been described as the 'ligaments utéro-lombaires' (Vallin), or 'plicæ utero-lumbales' (Waldeyer). They are really produced by nerve cords passing down from the hypogastric plexus, near the sacral promontory, to the pelvic plexus on each side near the base of the seminal vesicle, or cervix uteri.

VIII. Between the lower portion of the ilio-pectineal line internally and the external iliac vein externally is a triangular area, bearing interesting relations to the vas deferens, the obliterated hypogastric artery, and the crural ring; this we have described under the name of the *trigonum femorale*.

SALMO SALAR. THE DIGESTIVE TRACT IN KELTS.
By J. KINGSTON BARTON, M.R.C.P. Lond. (PLATES VIII., IX.)

So few observations have been made on Kelts in recent times that the following notes, and especially the plates which illustrate them, will, I think, be of interest.

Having observed that the mucous membrane with its epithelium, even in the stomachs of kelts dying with salmon disease, was of a perfectly normal appearance when properly fixed with preservative, I obtained permission from the Conservators of the Hampshire Avon to kill and examine a well mended kelt, if I should meet with such when salmon-fishing in the spring.

On March 18th, 1901, whilst fishing at Ringwood on the Avon, about fifteen miles by water from the sea, and only a few miles below the highest point to which salmon ascend in this river, I hooked and killed a bright, clean, and well mended grilse kelt. The fish was a female, and weighed between 5 and 6 lbs. Parts of the digestive tract from each division were placed in formalin 10 per cent., and other parts in Flemming's solution.

The stomach was empty, and very little was contained in the upper part of small intestine; but in the lower or large intestine there was a manifest yellowish mucous material.

The liver was pale and of slightly yellow hue. There was a very evident bile stain all down within the intestinal tract.

The new ovaries were 3 inches long, 1 inch wide, and $\frac{3}{4}$ inch thick, the individual ova being very small. But, for the size of the fish and its manifest sparse diet, one was surprised to see the ovaries so well developed so soon after spawning.

There were some eight full-sized ova (each with a deep red spot) still unshed. These ova were within the abdominal cavity, close to the ovaries, and near the œsophagus. The presence of these ova confirmed the fact that the fish had spawned in the recent winter. The flesh of the fish was only of the very

slightest pink colour. The gills were beautifully clean, and free from any parasite.

The next day, March 19th, some of the contents of the rectum from the formalin fluid were placed under the microscope. There seemed to be a good many fat-globules amongst the debris of round cells, with shed epithelium, and many yellow crystalline bodies (lime salts). There were some threadworms near the anus. The columnar epithelium appeared to contain droplets of fat, but no confirmatory tests were used at this stage.

The contents of a pyloric tube were very full of lymphocytes and what looked like fat-cells.

The stomach was quite empty and its walls rugous.

(Recently, examining the contents of a pyloric tube from a tidal kelt, preserved also in formalin, on adding an alcoholic solution of Sudan iii, numerous droplets stained red came into view.)

As two of the slides depicted in the plate came from this fish (Avon kelt), and as I have been so struck by the appearance of what must be fat in the lacteal system, I have given the history of the fish fairly at length.

When comparing the sections from this up-river kelt with others from tidal kelts, I think the presumptive evidence is that these fish have all had food within recent times, but in very sparing quantities.

In all cases the stomach has been found quite empty and contracted, showing no very recent feeding, yet there was just sufficient material in the lower bowel to confirm the suspicion that food has been digested. The cross-section of a tapeworm lying within the small intestine of a tidal kelt shows that this nematode, at all events, has been absorbing fat from its host (osmic acid stain, see fig. 5).

It is not at all unnatural to suppose that after the long physiological fast the fish only takes food in small quantities, at infrequent intervals, whilst on its way back to the sea.

Curiously, I do not find it at all easy to stain the *bona fide* fat absorption in hearty-feeding trout or samlets. But the intestine of a salmon from the nets, stuffed full of herring in all stages of digestion, shows the fat-cells accumulated in a similar manner in the lacteal region of the villi. This particular specimen

(fig. 3) had, of course, undergone post-mortem changes before being placed in Flemming's solution.

Where only fish food has been partaken of, it is important to realise how difficult it is to detect any undigested food-remains in the contents of the lower bowel, digestion is so complete.

It is only in trout, where so many flies, beetles, etc. are swallowed, that numerous undigested particles are easily seen, or in the case of many sea fish which feed on shellfish and crustacea.

Lymphocytes and fat-globules make up the bulk of faeces in fish that feed only on fish.

It has occurred to me that in the early days of the kelt stage the fish may very well thrive on infusoria or other low forms of aquatic life; for it is very evident that kelts do not feed with the frequency that sportsmen would have us believe.

However, these figures will speak for themselves, as showing that there is a fat-staining body where fat should be found in a fish that has digested fatty foods.

DESCRIPTION OF FIGURES.

PLATE VIII.

Fig. 1. The pyloric tube of the Avon river kelt; fixed in Flemming's solution six days, then washed and cut after being embedded in paraffin. Saffronin used as the counter-stain.

Note that the osmic acid stain is chiefly confined to the deeper parts or circumference of the lacteal system. This applies to the whole of the tube, and is exactly the same in five similar tubes. This would look as if no food had been absorbed very recently, and coincides with the fact that the stomach and duodenum were empty. Further, this section shows no signs of any recent desquamation of mucous coat.

Fig. 2. The small intestine from the same fish as in fig. 1. Similarly fixed and stained. Here the fat-globules are nearer the epithelial coat, but are not so numerous or intense as in the pyloric tubes. The food yielding fat cannot have been large in amount, as the tubes would appear to have absorbed the greater portion, leaving only a scanty amount to be taken up in the small intestine. It is very probable neither of these specimens were left long enough in the Flemming's solution.

Fig. 3. The small intestine from a well-fed fresh-run salmon taken in the nets, and purchased from Billingsgate. As the fish had been dead a good many hours before being placed in a preservative fluid (Flemming), there has been much post-mortem change, giving the same appearances as the so-called desquamative catarrh. In the similar lacteal positions are seen the fat-droplets. The stomach and intestines of this fish were stuffed with the remains of numerous herring in every stage of digestion. It was interesting to note that soon after the duodenum is passed, it is by no means easy to recognise any of the food-remains under the microscope, except as an emulsion of fat-cells and round-cells. All the bones and even scales of the fish swallowed are nearly completely dissolved before the contents of the stomach enter the intestine.

The naked-eye examination of the digestive tract in fish, coupled with a small pocket lens, gives more satisfactory results where there are any appreciable food-remains.

The microscope is more valuable for the histological examination of the tissues concerned with digestion outside the muscular coat. Note the large fat-globules in the mesentery in this section.

Fig. 4. The pyloric tube of a tidal kelt fixed in formalin 10%, afterwards washed and placed in Flemming's solution. The stomach of this fish was empty; but there was bile in the gall-bladder, and also within the small and large intestines. There was a fair amount of material (? true fæces) in the rectum. The amount of fat-cells stained with the osmic acid in this specimen is suggestive of much more recent feeding than is noticed in the river kelt (figs. 1 and 2).

The fact that fat-cells will stain with osmic after being fixed in formalin is a valuable discovery, as osmic acid alone is not at all a good fixer, nor is Flemming's solution so satisfactory as formalin 10%.

Owing to the price of osmic, it is also much more economical to fix first with formalin.

This specimen is from a well mended tidal kelt of the month of April, and taken three miles from the sea, in a large estuary.

The stomach and upper intestine being empty, will probably account for no fat-stains being found in the cylindrical epithelium itself.

Fig. 5. The small intestine of a well mended tidal kelt taken in the middle of May, close to the sea. A still greater amount of fat-cells is seen all through the lacteal system. In only one place are droplets seen in the epithelium of the mucous coat. It seems impossible that the osmic acid should not stain the remains of recent fat food absorption in this specimen.

Fig. 6. The pyloric tube of a brown trout (river Kennett), taken on fly, May 30th. This fish was stuffed with insects, flies, grubs, etc. innumerable, yet although dropped into Flemming's solution within two minutes of capture, the fat-cells in lacteal system are well stained,

but it cannot be found in the columnar epithelium excepting in one small group of columnar cells.

I have examined several other well-fed fish, and find it almost impossible to fix the fat-droplets in the epithelium, as usually described in text-books. In a smolt from the Welsh Dee, I have succeeded in fixing the fat-droplets in the epithelium. I think it requires a very small piece of tissue to be frequently changed into large quantities of Flemming's solution to get really satisfactory results. But the examination of figures 3 and 6 make it fairly certain that the osmic acid staining of the lacteal system in kelts shows that there has been food absorption.

PLATE IX.

Fig. 7. Collotype photo from the same fish as fig. 5. The black staining by osmic acid is very well seen in every area of the lacteal system in this well mended kelt.

Fig. 8. Collotype photograph from the same section as fig. 1—the Avon kelt. The osmic acid staining is very marked in the deeper parts of the lacteal system in this kelt (up-river, and early in the year).

I do not wish to dogmatise concerning these specimens, but having prepared these slides under the belief I would not find any such evidence of the presence of fat within the lacteal system, I hope other observers will take up the subject with greater skill and more time than I can command.

I believe a more recent theory has been expounded—that the intestines secrete fat apart from absorbing it; and it is also said that osmic acid stains only one constituent of fat. It may be that the empty fat-cells of the recently starved kelt have the property of staining very freely with osmic acid, and that these sections only indicate an ample readiness to absorb fat, rather than that it is proof of fat itself being there. I hope to continue these studies, and perhaps in the future to throw more light on these interesting points. Or, better still, more capable workers than myself may take the hint, and give us more definite information.

I may state that from January to middle of May this year (1901) I have had the opportunity of examining a few specimens of sea trout and salmon kelts, diseased and healthy, during each month, and from upper waters to tidal. Although the total number of such specimens is few, yet it is noteworthy that the stomach has always been absolutely empty. Bile has also been invariably present both in the gall-bladder and as a well marked stain in the intestine; yet the contents of the intestines in all cases has been so small, that if food has been partaken of, it must have been very meagre in quantity.

I am in hopes that the details of this particular series, which all came from the same river, may be published elsewhere.

**SOME OBSERVATIONS ON THE ORIGIN AND NATURE
OF THE SO-CALLED HYDATIDS OF MORGAGNI
FOUND IN MEN AND WOMEN, WITH ESPECIAL
REFERENCE TO THE FATE OF THE MÜLLERIAN
DUCT IN THE EPIDIDYMIS. By JOHN H. WATSON,
M.R.C.S., *late Holt Fellow, University College, Liverpool;
Assistant Demonstrator of Anatomy, London Hospital.***

IN this communication I intend to consider the fate of the Müllerian duct in man first, since not only can one trace it definitely with the aid of the microscope, but by eliminating the foetal residues likely to remain in connection with it, one is able to study with less chance of confusion the more complicated vestigial structures that are linked together with the Wolffian duct.

Most anatomical text-books state that tacked on to the testicle are two hydatid bodies, one having a pedicle, the other being without; and the sessile body is described as a derivative of the Müllerian duct. Now, in order to corroborate this last statement, I have made a considerable number of microscopical sections of testicles with the epididymis attached, the results of which are here stated as briefly as possible; and although very little, if anything, new has been made out, the work is interesting I think, in that it confirms the observations published by Löwe and Roth on the continent some time ago.

The Sessile Hydatid of the Testicle.

Before entering into the microscopical details, it will be worth while to note the macroscopical peculiarities of the sessile hydatid. After examining a large number of testicles, my own experience is that the sessile hydatid is much more frequently present than the pedunculated one; moreover, instead of being transparent and bladder-like, as its name implies, one

finds it to be a firm, fleshy body, the extremity of which appears to be in some cases drawn out into several very small tag-like processes; hence one is inclined to agree with Testut that in every sense of the word 'hydatid,' this body is misnamed. With regard to its exact position, it is fixed by a broad base to the upper pole of the testicle, the caput epididymis overlying it slightly; and a connection in the form of a band of tissue, over which the visceral tunica vaginalis is raised as a fold, is often to be observed between the two.

FIG. 1.—Section through sessile hydatid and adjacent parts of testis and epididymis (7 months foetus).

A, persistent Mullerian duct in centre of hydatid; B, testis; C, epididymis.

FIG. 2.—Section of sessile hydatid (8 months foetus).

a, testis; b, hydatid; c, circumferential layer of cuboidal epithelium; d, concentrically disposed wall of Mullerian duct; e, lumen (tri-radiate) of duct lined with columnar epithelium.

The microscopical appearances of these bodies, of course, differ greatly according to the age of the subject from which they were obtained.

In all sections of foetal testicles between the ages of 7 to 9 months, remnants of the Mullerian duct could be traced running along the anterior and outer border of the epididymis. The younger the testicle, the more obvious this solitary tubule appears, around which the neighbouring connective tissue is arranged concentrically.

The micro-photographs appended were taken of sections of the testicle of an eight months foetus, which possessed a sessile hydatid only. The degenerate remains of the duct are visible in the epididymis, and as the sections approach the caput epididymis, there is a gradual dilatation of its lumen, which becomes very evident in a section across the hydatid (*vide* fig. 2), where it assumes a tri-radiate appearance. The hydatid itself consists of a groundwork of fibro-cellular material, which has a very noticeable concentric disposition around the centrally situated vestige of the Müllerian duct, whereas the periphery of the body is invested by a single layer of columnar epithelium. In one series of sections of the testicle of a 7 months foetus,

FIG. 3.—Section through body of epididymis (8 months foetus).

A, Müllerian remnant in anterior border; B, epididymis; C, testis.

I was so fortunate as to get a section showing the communication of the duct with the exterior, *i.e.*, with the processus vaginalis. In making sections towards the tail of the epididymis, vestiges of the Müllerian duct are more difficult to recognise; in fact, it is not always possible to see a trace below the body of the epididymis, even in full-term foetuses.

As one examines in this manner serial sections of the testicles of subjects of gradually increasing age, the evidences of the Müllerian duct are more and more difficult to see. For instance, in some sections of the epididymis of a boy aged 12, after very careful scrutiny, a doubtful collection of degenerate cells was made out in the position where the Müllerian

remnants should occur, and in close proximity one or two small vessels were placed, round both of which the connecting tissue was arranged in a circular manner; but in all sections of adult epididymes submitted to the microscope, not a single trace of the duct itself was visible, but in its place, as a rule, a few minute vessels were observed, embedded in the connective tissue, which is abundant in the prominent anterior border. The collection of fibro-cellular tissue at this point is interesting from an embryological standpoint, for into it is fused all that practically remains of the mesosalpinx, a structure that is very well marked during the third and fourth months of foetal life. Sections of sessile hydatids taken from middle-aged and old people show nothing of the original structure of the Müllerian duct, except perhaps the lumen of the tube. This may appear as a single fissure or several smaller fissures, situated centrally, and devoid of any distinctive epithelial lining. The epithelium appears to degenerate, the opposite sides of the lumen come together, eventually fusing, and thus one can account for the presence of the multiple lumina which may be present.

No evidence whatever of the Müllerian duct is to be found in sections of an adult spermatic cord, nor have I seen any distinct trace of it in the cords of still-born infants examined microscopically.

Now one can leave the discussion of this sessile body, and treat with advantage the relationships and structure of the pedunculated hydatids, dealing first with that found in the female.

The Pedunculated Hydatid found in Females.

This, according to Quain, is "a pedunculated cyst, known as the hydatid of Morgagni, apparently peritoneal in origin, and frequently found attached to one of the fimbriæ, or to the tube itself." Again, most gynæcologists invariably refer to the same body as a "cyst of Kobelt." This double nomenclature, so to speak, is very unfortunate, and confuses one greatly when running through the literature.

With regard to the exact position of these pedunculated

bodies, my own experience differs from that set down by Quain. In those cases in which it was present—about 50 per cent. of all examined—it was never seen connected with one of the fimbriae of the Fallopian tube, and it is the exception to find it completely blended at its base with the tube. Usually, however, it appeared to come from the anterior layer of the mesosalpinx, the pedicle by which it is attached springing from this layer at a spot 1 cm. or thereabouts from the fimbriae ovaricae, and practically opposite its centre, *i.e.*, a point midway between its base and apex. The length of the stalk itself varies greatly in different women, and even on opposite sides of the same

FIG. 4A.—Diagram of uterus and appendages (child 3 years).

- 1, cervix uteri; 2, broad ligament; 3, edge of broad ligament; 4, ovarian fimbria; 5, cyst at base of ovarian fimbria; 6, Fallopian tube; 7, mesosalpinx; 8, Cowper's uteri; 9, Wolffian duct (remnant); 11, collecting tube; 13, fimbriae of tube; 15, hydatid stalk; 16, hydatid of Morgagni; 17, ovary; 18, round ligament.

individual. On a closer inspection, its proximal end is seen to be in continuity with the collecting tube (Wolffian duct proper) of the parovarium (*vide* fig. 5). Moreover, in a well marked specimen the proximal end or base of the stalk is connected by a ridge-like fold with the Fallopian tube, a second fold apparently running into one of the mesonephric tubules. These ridges being continued into the pedicle of the hydatid, give it a doubly infolded appearance (*vide* fig. 6) on one aspect, the other aspect of this band-like structure is quite even. The upper and lower margins merge into the aforesaid ridges, and there is a gradual tapering of the stalk as it approaches the cyst. In the rare instances in which I have seen a pedunculated

hydatid arising in the immediate vicinity of the fimbriated extremity of the Fallopian tube, a distinct connection through the broad ligament with the rudimentary Wolffian duct could always be made out with a good lens, if not with the naked eye.

The Hydatid Cyst.

In dealing with the cyst, one notices that it assumes many forms; it may be a unilocular sac, a cyst with partial constriction into two compartments, or a couple of separate small cysts may exist. The size appears to increase slowly up to puberty, when it may equal that of a pea, or even a cherry. As a rule, they do not become any larger; in old age they seem to become much smaller, in some cases almost to shrivel away.

And here I would call attention particularly to a small apparently mucous cyst which appears at the base of the fimbria ovaricae (*vide* fig. 4A), and is quite as frequently present as the hydatid cyst itself. How to account for its appearance is a difficult matter. If one considers it to be a simple retention cyst of a mucous gland, then the question arises, why is it always found in this particular spot, and usually in association with a similar cyst at a corresponding point in the opposite broad ligament? My first impression was that it might be a stalkless hydatid of Morgagni, but this idea was discounted by the fact of there being present in the same case, as a rule, a well marked pedunculated cyst (fig. 4A). A plausible suggestion is, that the duct of a large mucous gland at the ostium abdominale, lying contiguous to the ovarian fimbria, is very liable to be kinked owing to the drag of the ovary, and thus the lumen of the duct being occluded, a cyst forms. Even this, however, is a mere theory, and lacks microscopical investigation. There can be no doubt, however, that it is frequently taken for the hydatid of Morgagni, which is an entirely different structure.

The Parovarium (Organ of Rosenmüller).

A brief reference to the parovarium here will help perhaps in following out the sections described later.

It is comprised of a series of rather straight and parallel tubules lying in the mesosalpinx. To these the term 'efferent' has been applied. Their number varies between 15-20. They are connected by one extremity with a broader tube running parallel almost and just below the Fallopian tube, which is known as the 'collecting tube' (it is a remnant of the Wolffian duct proper); the other extremity stretches towards the hilum of the ovary. Of these efferent tubules, it is needless to say that both the upper and lower end of the series gradually

FIG. 4.—Section across collecting tubule.

- 1, hydatid stalk ; 2, fibro-muscular tunic ; 3, tubule in transverse section ;
4, broad ligament ; 5, accompanying artery in section.

become shorter and crowded together, more especially the former. Roth has described a duct which he calls the 'tubo-parovarium,' a vestigial canal joining the collecting tube of the parovarium with the Fallopian tube—a condition of things that I have searched for in vain so far.

A section across the collecting tube shows a most remarkable appearance under the microscope (*vide* fig. 4): instead of seeing a comparatively simple tubular structure, one observes numerous tubules cut across with well defined walls. The lumen of each is lined by—

- (1) A single layer of columnar cells, which is surrounded by
- (2) A very thick layer of cells, polyhedral in outline, evidently involuntary muscle in cross-section.
- (3) Outside this again is a coat of involuntary muscle, disposed circularly, altogether a much thinner layer than the previous

one: each tubule is separated by a varying amount of inter-tubular connective tissue.

(4) The entire collection of tubules is practically encapsuled by a fibro-muscular tunie.

In concluding the description, one must not forget to notice the large vessels (artery and vein) lying in close proximity. The whole structure reminds one of a section of the epididymis in the male (even to the artery to the vas deferens), with which it practically corresponds. One, of course, must make allowances, when comparing, for the deficiencies in the sections of the collecting tube, in that one is dealing with a functionless, and

FIG. 5. —Section at the point of fusion of hydatid pedicle with collecting tube.
1, broad ligament; 2, hydatid stalk; 3, collecting tubule; 4, parovarian vessels;
5, intervening fibro-muscular tissue; 6, almost complete tubule in hydatid stalk; 7, vessels of hydatid.

hence much atrophied Wolffian duet, whereas in the male it has attained its highest development. When a section is examined as close as possible to the point at which the base of the hydatid stalk enters the broad ligament, one sees that the hydatid pedicle and the encapsuled collecting tubule are practically superimposed (fig. 5); that in the pedicle itself similar tubules transversely cut, but much more atrophied than those described as part of the much coiled Wolffian or collecting tube, are visible. Again, each of these structures is accompanied by a large artery and vein; moreover, at this point (*vide* fig. 5) they are separated by an intervening bundle of fibro-muscular tissue. A section a little nearer the uterus

shows the disappearance of this intervening tissue, and the fusion of these two structures with one another, even to the junction of the accompanying vessels.

In minutely investigating the pedicle, the infolded character (previously referred to) of one surface is very well shown (fig. 6), but the most noticeable feature is the large artery and vein in its midst, and disposed around these are some very scattered and partially obliterated tubules, with a very sparse coating of involuntary muscle, which I consider to be the remains of the continuation of the collecting tube, or rather

FIG. 6.—Section of hydatid stalk (from female) near its point of emergence from broad ligament.

1 peripheral fibro-muscular layer ; 2, atrophied tubules ; 3, large central vessels ; 4, broad ligament (adjacent).

Wolffian duct proper, into the pedicle. These tubules, moreover, are dotted about in a groundwork of fibrous connective tissue. As one examines more and more distal sections (*i.e.*, nearer the cyst) their number decreases, and the more evident their degeneracy appears, until they, to all intents and purposes, vanish. A more remarkable feature is the continued large size of the artery and vein. Surrounding these vestigial structures is a curious layer extending right round the periphery, and composed of involuntary muscle fibres, with a large admixture of somewhat dense fibrous tissue. The surface of the pedicle has an endothelial lining.

The Histology of the Cyst.—The microscope reveals its wall to comprise a single layer of cuboidal nucleated epithelium, resting on a layer of fibrous tissue, in which a small quantity of involuntary muscle is interspersed. This layer varies greatly in thickness, depending to a large extent upon the amount of distension. A point which has been much discussed is the character of the epithelial lining. Fleischl, Ballantyne, and Williams regard it as ciliated. Klob and Kölliker aver that it is flattened pavement epithelium. My own experience is as quoted above, with one exception found in a cyst taken from a

FIG. 7.—Section of hydatid stalk close to cyst.

1, ridges noted in text; 2, atrophied tubules; 3, central vessels; 4, peripheral fibro-muscular layers.

child which had a lining of ciliated epithelium. Previously I had confined my attention to specimens taken from adults; possibly there is a tendency for the cilia to disappear with advancing age, and the epithelium to change its character owing to increased tension. Before making any definite statements as to the exact nature of this cyst, it will be well to refer to the *pedunculated hydatid* found in the male.

The Pedunculated Hydatid of the Male.

This body, when present, which by the way is the exception rather than the rule, is attached by a short pedicle close to the

apex of the caput epididymis, *i.e.*, roughly to the upper end of the Wolffian duct, from which, of course, the epididymis is developed in part, and therefore, comparatively speaking, it is placed in a position identical with that of the hydatid body in the female. The dimensions of this cyst are subject to much variation; it is certainly much smaller than that found in women. The histology of the cyst wall is simply a lining membrane of beautiful cuboidal or columnar celled epithelium—(my own observations lead me to think the ciliated epithelium of other writers a variable quantity)—here again lying on a fibrous

FIG. 8.—Section of cyst of pedunculated hydatid. (Micro-photograph.)

1, lumen of cyst; 2, loculus; 3, layer of columnar epithelium; 4, fibrous wall.

muscular wall (fig. 8). Of the structure of its pedicle at the present moment I greatly regret being unable to say anything definite, as my efforts to obtain reliable sections have been failures, more especially since at the present time the question of the homologies of these pedunculated bodies in the male and female is a vexed one. For instance, to cite two of the most recent anatomical text-books, *viz.*, Testut and Poirier, the former definitely states they are homologous structures, whereas H. Rieffel, writing in Poirier's treatise, says, that owing to the uncertainty of their embryological origin it is impossible to make a final statement.

The arguments in favour of the identity of the pedunculated bodies in the male and female are—

(1) The fact that the pedicles arise from corresponding points in both sexes, as previously stated.

(2) The histological structure of the cyst wall in both sexes is identical.

(3) The differences in regard to the length of the hydatid pedicle in the male and female may be accounted for by—

(a) an embryological.

(b) a mechanical factor.

(a) In all embryos of the 3rd or 4th month there is a well marked mesosalpinx, and it must be remembered that in the female this undergoes great development, the hydatid and its stalk growing conjointly with it, whereas in the male it rapidly and almost entirely disappears.

(b) Here one refers to its more dependent position in a woman's pelvis, hence the tendency to elongate; in man it rests upon the upper pole of the testis, so that tension is relieved, and there is every facility for complete atrophy.

A yet more important problem still is to explain their origin. To do this, numerous and diverse theories have been propounded, the more important being based on embryological grounds. For present purposes they may be cut down to the following four, since they are perhaps the most frequently put forward.

The pedunculated hydatid may be—

(1) A reduplication of a peritoneal fold;

(2) A relic of the pronephros;

(3) The ampullated extremity of the Wolffian duct;

(4) A cystic condition of one or more of the mesonephric tubules.

To discuss these briefly:—

No. 1 theory has been put down from the fact that it appears in a standard English anatomical work; but there can be no hesitation in saying, from what we have already seen, that the statement is not well founded.

No. 2. The pronephric origin is supported by such authorities as Gegenbaur, Roth, and others.

The arguments in its favour shortly are:—

A. The pronephros is a purely secretory organ, consisting of

a series of tubules (nephrostomes), communicating, on the one hand, with the coelom, on the other with the Wolffian duct, and having, of course, a glandular lining of non-ciliated cells (Kollmann). In the process of development the coelomic opening is closed, and later the functionless Wolffian duct is obliterated, but the secretory function of the pronephric tubules persisting, causes the cystic formations.

B. The histological structure, *i.e.*, the fact of there being a non-ciliated instead of a ciliated epithelial lining, which one expects to find in Wolffian derivatives, and moreover the apparent isolation of the cyst from the remaining mesonephric tubules, is, if anything, evidence in its support.

C. Lastly, many authorities (Minot) consider the duct of the pronephros continuous with the upper end of the Wolffian duct; and, so far as one can say at present, the vestiges of the duct seen in sections of the hydatid pedicle may be equally either Wolffian or pronephric.

The above reasons seem to me now unconvincing, and outweighed by the cons tabulated below.

Reasons against:

(1) The presence of a pronephros in man is now denied by most authorities.

(2) The Müllerian duct is said to be the duct of the pronephros (Rossmann, Ampt, and Berry Hart); and therefore if any pronephric remains are present, they should be connected with it, and not with a pedicle containing traces of the Wolffian duct.

(3) The fact that many authorities maintain the cyst has a lining of ciliated epithelium. This, of course, is really a minor consideration, and one with which my own experience does not agree, but it is very probable that it occurs in the cysts taken from young children.

(4) Lastly, what I consider to be a point of importance is the continuation of the blood-vessels accompanying the Wolffian duct right up to the cyst itself. Had the cyst been derived from a pronephric tubule, its blood supply ought to have come from an entirely different source.

The arguments here quoted against the pronephric theory may be adduced in favour of their Wolffian origin, so that one

has now, I think, no alternative but to decide between the two remaining suggestions, viz.—is it the remains of the ampullated extremity of the Wolffian duct, as originally set forth by Kobelt, an idea that has had the support of Luschka and Hennig; or is it simply a cystic mesonephric tubule, as contended by such authorities as Kobelt, Follin, Rokitansky, Henle?

In favour of the latter view is the fact that we sometimes see two cystic bodies tacked on to the hydatid pedicle (assuming that it contains the upper end of the Wolffian duct); and it is practically certain that the anterior extremity of the Wolffian duct is not bifid (*vide* fig. 1); but again, if we grant its origin from a mesonephric tubule, it is difficult to understand why they should be isolated from the main body of the mesonephros; so it is impossible to say even now from which of the two the hydatid is derived, although one must not forget that it is not unlikely that it may be developed from either.

CONCLUSIONS.

The general statement as to the Müllerian origin of the so-called sessile hydatid is undoubtedly correct, for by the aid of microscopical sections it is possible to find remnants of the Müllerian duct in male fetuses and children, and even to trace it along the anterior and outer border of the epididymis, right into the hydatid itself.

To elucidate the nature of the pedunculated hydatids is a much more difficult undertaking, for although the literature on the subject is exceedingly profuse, it can only be described as chaotic; therefore, in recording my own observations, I have looked upon that pedunculated cyst which occurs the most frequently as the true hydatid of Morgagni, *i.e.*, a small cyst, having a stalk of variable length, which usually springs from the anterior layer of the mesosalpinx, occasionally from the fimbriated extremity of the Fallopian tube, and which can invariably be traced to the parovarium through the broad ligament. This pedunculated cyst is the homologue of the stalked hydatid attached to the epididymis of the male, both

being derivatives of either the mesonephros or the anterior end of the Wolffian duct. The cyst occurring at the base of the fimbria ovarica is of doubtful origin, possibly a distended mucous gland, or a cyst of the tubo-parovarian duct; but further investigation is needed to settle this question.

Finally, the complicated nature of the collecting tube of the parovarium, and its similarity on section to the structure of the epididymis, is a very interesting feature, and one alludes to it here again because it is a fact of which apparently very little notice is taken in anatomical works.

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HYOID APPARATUS IN MAN, IN WHICH A SEPARATE
EPI-HYAL BONE WAS DEVELOPED. By Professor
Sir WILLIAM TURNER.

SOME years ago I obtained in the dissecting-room a specimen which illustrates a very unusual modification in the hyoid apparatus in man. On the right side of a male subject, the styloid process, 31 mm. long, was from two to three times as thick as is customary; and instead of ending in a point, formed an expansion, 13 mm. in antero-posterior, and 9 mm. in transverse diameter. Below, and articulated with it by a movable joint, was a bar of bone, 56 mm. long, which passed downwards to articulate with the small cornu of the hyoid. This bar was thickest at its upper end, and measured 10 mm. antero-posteriorly and 8 mm. transversely, whilst at the lower end its dimensions were only 4 by 3 mm. The small cornu was somewhat thickened, and had its usual articulation at the junction of the body with the great cornu of the hyoid, which parts of that bone had their customary appearance. When the right hyoid arrangement in this neck is compared with the normal condition in a dog, the bar of bone is seen to be the homologue of the epi-hyal bone in this and many other mammals. There was no vestige of a right stylo-hyoid ligament, the place of which had been taken by the epi-hyal.

On the left side the styloid process was 50 mm. long, and terminated below in a point from which the stylo-hyoid ligament, 30 mm. long, passed downwards to end in the small cornu of the hyoid, 16 mm. long, which had the customary attachment below to the hyoid. On this side the hyoid apparatus may be regarded as normal, although the small cornu was several mm. longer than one usually sees. It should also be stated that at its base, in the region of the tympano-hyal bone, described by Sir Wm. Flower, the styloid process was much thicker than usual.

In skulls where the styloid process is greatly elongated, one

sometimes sees a thickening about half down its length, which looks as if, at one time, the lower moiety had been developed independently of the upper, and that when they became fused together, the bone had thickened around the place of fusion. If this is the correct explanation, the lower moiety is presumably an ossification in the stylo-hyoid ligament, and represents an imperfect epi-hyal, which had been connected at one end by unossified ligament to the small cornu of the hyoid, and by the other had fused with the styloid process.

THE ORIGIN OF VERTEBRATES, DEDUCED FROM
THE STUDY OF AMMOCETES. By WALTER H.
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PART X.—ON THE ORIGIN OF THE AUDITORY ORGAN; THE MEAN-
ING OF THE VIIIth CRANIAL NERVE; TOGETHER WITH A
CONSIDERATION OF THE ORIGIN OF THE CRANIAL NERVES AS A
WHOLE, IN ACCORDANCE WITH THE PRINCIPLES LAID DOWN IN
PART I.

IN the course of these papers I have discussed the origin of all the cranial nerves with the exception of the VIIIth pair, and have shown how they, one and all, may have been derived from corresponding nerves of an arthropod ancestor. I have left the discussion of the origin of the auditory nerves to the end for various reasons, the chief of which is, that their position in the vertebrate cranial series is not so clearly defined as that of the other cranial nerves.

By the general consensus of morphologists at the present time, the auditory apparatus arose as a specially developed member of a series of segmental sense organs, which were originally closely related to the branchiæ, and in position were neither ventral nor dorsal, but lateral. The same opinion has also been held with respect to the olfactory organ, so that the conception has arisen that the ancestor of the vertebrate was an animal which possessed a segmental series of branchial pouches and gill slits, not only in the opisthotic, but also in the pro-otic region of the head. As has been pointed out again and again in this series of papers, such a conception is fatal to common-sense, and is totally unnecessary; for the natural branchial unit is not a space or pouch, but the substance between the pouches, i.e., branchiæ-bearing appendages.

With such a branchial unit, it follows that the branchial sense organs may be considered as special lateral organs belong-

ing to the mesosomatic branchial appendages, and that all the appendages in front of the mesosomatic may have had homologous sense organs without any necessity of bearing branchiæ. Thus I have shown how, in accordance with my theory, the olfactory organ arose from special sense organs which originally belonged to the first pair of antennæ, and not to any branchial segment; so also the auditory organ may have arisen in connection with the non-branchial prosomatic appendages or the branchial mesosomatic, and yet in either case be in perfect harmony with the morphological conception that it belongs to the same series as the branchial sense organs.

At present neither the anatomical nor morphological evidence is sufficient to enable us to state definitely to which segment the auditory nerve belongs. According to many observers it apparently represents a separate segment, just as the special sense organs of the scorpion, known as the pectens, apparently represent all that remains of a separate pair of appendages; according to others, it is the nerve of a special sense organ belonging to one of the splanchnic segments, although it is impossible to state whether that segment is represented by the VIIth nerve or not.

It is not possible to determine its segmental position by the evidence of its origin in the central nervous system, for clearly the so-called sensory centres have not the same significance in this respect as the motor centres; the nerve cells belonging to the sensory nerves, which indicate segments, are those of the ganglia of the dorsal roots, not the sensory ganglia in the central nervous system. This last criterion, as far as it is of any value at all, points to the conclusion that the auditory segment belongs neither to the facial nor to the trigeminal group of nerves, for there is never the slightest sign of fusion between the peripheral ganglion of the auditory nerve and that of the facial or trigeminal.

Judging from the clear evidence of *Ammocetes*, that the facial nerve supplies the foremost segments of the respiratory chamber, and belongs therefore to the mesosomatic group of nerves, and also from the position of the cartilaginous auditory capsule, formed as it is in connection with the parachordals, *i.e.*, with cartilaginous bars situated between the prosomatic tra-

beculæ and the mesosomatic branchial basketwork, I conclude that the origin of the auditory apparatus must be sought for at the junction between the prosoma and mesosoma, without being able to say definitely whether it belonged originally to a prosomatic or mesosomatic segment.

The upholders of the view that the vertebrates are descended from annelids consider that the series of segmental sense organs, from one of which the auditory organ arose, are represented in the annelids by the segmentally arranged lateral sense organs, such as have been described by Eisig¹ in the Capitellidæ.

"There are many reasons," says Lang,² "for considering these lateral organs to be homologous with the dorsal cirri of the ventral parapodia of other Polychæta, and in the family of the Glyceridæ we can follow, almost step by step, the transformation of these cirri into lateral organs." Eisig describes them in the thoracic præbranchial region as slightly different from those in the abdominal branchial region; in the latter region the ventral parapodia are gill-bearing, so that these lateral organs are in the branchial region closely connected with the branchiæ, just as is also the case in the vertebrates. It is but a small step from the gill-bearing ventral parapodia of the annelid to the gill-bearing appendages of the phyllopod-like Protostracan; so that if we assume that this is the correct line along which to search for the origin of the vertebrate auditory apparatus, then, on my theory of the origin of vertebrates from a group resembling the Protostraca, it follows that special sense organs must have existed either on or in close connection with the branchial and præbranchial appendages of the Protostracan ancestor of the vertebrates, which would form an intermediate link between the lateral organs of the annelids and the lateral and auditory organs of the vertebrates.

Further, these special sense organs must not have been mere tactile hairs, but must have possessed some special function, and their structure must have been compatible with that function. What that function must have been is pointed

¹ Eisig, "Die Seitenorgane u. becherförmigen Organe der Capitelliden," *Mitth. a. d. Zool. Stat. z. Neapel*, vol. i. p. 278, 1879.

² Lang, *Text-Book of Comp. Anat.*, vol. i. p. 234.

out in an admirable manner in a series of papers by Lee. In his paper¹ on the function of the ear and lateral line in fishes he gives the reasons why he considers that an organ for the actual sense of hearing in the ordinary meaning of the term does not exist in water-living animals, but was developed in animals that took to living on land, out of an organ which had previously been formed entirely for equilibration purposes, especially the estimation of pressures. This organ was one out of many such organs, viz., those of the lateral line, and by direct experimentation he shows how the organs of the lateral line are concerned in equilibration and the co-ordination of movements, especially those of the fins. Lee's evidence, combined with that of Fuchs² and Breuer,³ is sufficiently strong to warrant the conclusion that the auditory and lateral line organs were originally special sense organs concerned with equilibration, and perhaps especially with the estimation of water pressure.

Throughout these papers the evidence which I have put forward has in all cases pointed to the same conclusion, viz., that the vertebrate arose by way of the Cephalaspids from some Arthropod, either belonging to, or closely allied to, the group called Palæostraca, of which the only living representative is *Limulus*. If, then, my argument so far is sound, the appendages of *Limulus*, both prosomatic and mesosomatic, ought to possess special sense organs which are concerned in equilibration or the appreciation of the depth of the water, or possess some modification of such function, and among these we might expect to find that somewhere at the junction of the prosoma and mesosoma such sense organs were especially developed to form the beginning of the auditory organ.

Now, it is a striking fact that the appendages of *Limulus* do possess special sense organs of a remarkable character which are clearly not simply tactile; thus Gegenbaur,⁴ as already mentioned by me, has drawn attention to the remarkable branchial

¹ *American Journ. of Physiology*, vol. i. p. 128.

² Fuchs, "Ueber der unten den Haut liegenden Canalsystem bei den Sela-chiern," *Arch. f. d. gesam. Physiol.*, vol. lix. p. 454, 1895.

³ Breuer, "Ueber die Function der Otolithen-Apparate," *Arch. f. d. gesam. Physiol.*, vol. xlviii. p. 195, 1890.

⁴ *Abhandl. d. Naturforsch. Gesellschaft z. Halle*, Bd. iv., 1858.

sense organs of *Limulus*; and Patten¹ has pointed out that special organs, which he considers to be gustatory in function, are present on the mandibles of the prosomatic appendages. I myself, as mentioned in my address to the British Association at Liverpool in 1896, searched for some special sense organ at the junction of the prosoma and mesosoma, and was rewarded by finding that that extraordinary adjunct to the last locomotor appendage, known as the flabellum, was an elaborate sense organ. In this paper I propose to show that all these special sense organs are constructed on a somewhat similar plan; that the structure of the branchial sense organs suggests that they are organs for the estimation of water pressures; that among air-breathing arthropods sense organs built up on a somewhat similar plan are universally found, and are considered to be of the nature of auditory and equilibration organs; and, what is especially of importance in view of the fact that the most prominent members of the Palæostraca were the sea scorpions, that the remarkable sense organs of the scorpions known as the pectens belong apparently to the same group.

The Poriferous Sense Organs of the Appendages in Limulus.

On all the branchial appendages in *Limulus* special sense organs are found of a most conspicuous character. They form in the living animal bluish convex circular patches, the situation of which on the appendages is shown in fig. 6, Part II. of this series of papers.² These organs are not found on the non-branchial operculum. They were originally described by Gegenbaur, and I have already referred to them in Part III. of this series.³ Gegenbaur described how the surface of the organ is closely set with chitinous goblets shaped as seen in fig. 1A, which do not necessarily project free on the surface, but are extruded on the slightest pressure. Each goblet fits into a socket in the chitinous covering, and is apparently easily protruded by variations of pressure from within. The whole

¹ "On the Morphology and Physiology of the Brain and Sense Organs of *Limulus*," *Q. J. Micr. Sci.*, vol. xxxv. p. 1, 1893.

² *This Journal*, vol. xxxii. p. 563.

³ *This Journal*, vol. xxxiii. p. 185.

surface of the organ on the appendage is slightly bulged in the living condition, and the chitin is markedly softer here than in the surrounding part of the limb. Each of these organs is surrounded by a thick protection of strongly branching spines. On the surface of the organ itself no spines are found, only these goblets, so that the surface view presents an appearance as in fig. 1B. Each goblet possesses a central pore, which is the termination of a very fine, very tortuous, very brittle chitinous tubule, *ch.t.*, which passes from the goblet through the layers

18

FIG. 1.—A, a goblet from one of the branchial sense organs of *Limulus*. *ch.t.*, chitinous tubule. B, surface view of a portion of a branchial sense organ.

of the chitin into the subjacent tissue. The goblets vary considerably in size, a few very large ones being scattered here and there. The fine chitinous tubule is especially conspicuous in connection with these largest goblets. In the smaller ones there is the same appearance of a pore and a commencing tube, but I have not been able to trace the tube through the chitinous layers as in the case of the larger goblets. Gegenbaur in his picture draws a straight tubule passing from every goblet among the fine canaliculi of the chitin. He says they are difficult to

see, except in the case of the larger goblets. The tubule from the larger goblets is most conspicuous, and is in my sections always tortuous, never straight, as represented by Gegenbaur. A special branch of the appendage nerve passes to these organs, and upon the fine branches of this nerve groups of ganglion cells are seen, very similar in appearance to the groups described by Patten¹ on the terminal branches of the nerves which supply the mandibular organs. At present I can see no mechanism by which the goblets are extruded or returned into place. In the case of the Capitellidæ, Eisig describes retractor muscles by means of which the lateral sense organs are brought below the level of the surface, and he imagines that the protrusion is effected by hydraulic means, by the aid of the vascular system. In the branchial sense organs of *Limulus* there are no retractor muscles, and it seems to me that both retraction and protrusion must be brought about by alterations of pressure in the vascular fluids. Certainly the cavity of the organ is very vascular. If this be so, it seems likely enough that such an organ should be a very delicate organ for estimating changes in the pressure of the external medium, for the position of the goblets would depend on the relation between the pressure of the fluid inside the organ and that on the surface of the appendage. Whether the chitinous tubule contains a nerve terminal or not I am unable to decide from my specimens, but, judging from Patten's description of the similar chitinous tubules belonging to the mandibular organs, it is most highly probable that these tubules also contain a fine terminal fibre.

These organs, then, represent segmental branchial sense organs, of which it can be said, their structure suggests that they may be pressure organs, but the experimental evidence is at present wanting.

Passing now from the branchial to the prosomatic region, the first thing that struck me was the presence of that most conspicuous projection at the base of the last locomotor appendage, which is usually called the flabellum, and has been described by Lankester as an exopodite of this appendage. It is jointed on to the most basal portion of the limb (see fig. 12), and projects dorsally from the limb into the open

¹ *Op. cit.*, pl. 1, fig. 1.

slit between the prosomatic and mesosomatic carapaces, as is seen in fig. 2, *fl.* Of its two surfaces, the undermost is very convex and the uppermost nearly flat from side to side, the whole organ being bent so that when the animal is lying half buried in sand, entirely covered over by the prosomatic and mesosomatic carapaces, except along this slit between the two, the

n

FIG. 2.—The endognaths of *Limulus* pushed out of the way on one side in order to show the position of the flabellum (*fl.*) projecting towards the crack between the prosomatic and mesosomatic carapaces.

upper flat or slightly convex surface of the flabellum is exposed to any movement of water through this slit, and owing to its possessing a joint, the direction of the whole organ can be altered to a limited extent. The whole of this flat upper surface is one large sense organ of a striking character, thus forming a great contrast to the convex under surface, which is remarkably free from tactile spines or special sense organs.

The nerve going to the flabellum is very large, almost as large as the nerve to the rest of the appendage,¹ and the very large majority of the nerve fibres turn towards the flat upper-

sp

so

ch p bl n gl p ch

FIG. 3.—Section through flabellum. *ch.*, chitinous layers; *s.o.*, sense organs; *sp.*, spike organ; *p.*, pigment layer; *gl.*, ganglion cell layer; *bl.* and *n.*, blood spaces and nerves.

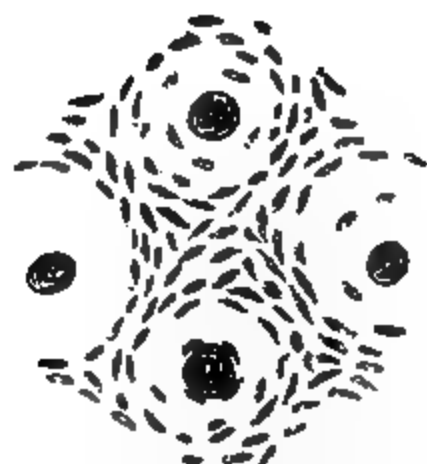


FIG. 4.—Section parallel to the surface of flabellum, showing the porous terminations of the sense organs and the arrangement of the canaliculi round them.

most side, where the sense organ is situated. Between the nerve fibres (*n.*) and the chitinous surface containing the special sense tubes are seen, as in fig. 3, masses of cells (*gl.*),

¹ It is worthy of notice that the four pairs of organs, the flabella in *Limulus*, the pectens in *Scorpio*, the halteres in the *Diptera* and the auditory vesicles in *Vertebrata*, the function of all of which, as suggested in this paper, is possibly similar, are all described as innervated by nerves of remarkable magnitude.

apparently nerve cells, which form a broad border between the nerve fibres and the pigmented chitinogenous layer (*p.*). On the opposite side nothing of the sort intervenes between the pigmented layer and the blood spaces and nerve fibres which constitute the central mass of the flabellum.

At present I am inclined to look upon this mass of cells as constituting a large ganglion, which extends over the whole length and breadth of the flabellum. At the same time my preparations are not good enough to enable me to trace out the connections of these cells, especially their connections with the special sense organs.

In fig. 5 I give a magnified representation of three of these flabellar sense organs in transverse section. As is seen, the section divides itself into 4 zones: 1, the chitinous layer (*ch.*); 2, the layer of pigment (*p.*) and hypodermal cells; 3, the layer of ganglion cells (*gl.*); and 4, the layer of nerve fibres (*n.*) and blood spaces (*bl.*). The chitinous layer is composed of the usual three zones of the *Limulus* surface: externally (fig. 5), a thin homogeneous layer followed by a thick layer of chitin (3) in which the fine vertical tubules or canaliculi are well marked; the external portion (2) of this layer is differentiated from the rest by the presence of well marked horizontal layers in addition to the canaliculi.

In this chitinous layer the special sense organs are found; they consist of a large tube which passes through all the layers of the chitin except the thin homogeneous most external layer. This tube is conical in shape; its base, which rests on the pigmented layer, being so large and the organs so crowded together that a section of the chitin across the base of the tubes gives the appearance of a honeycomb, the septa of which is all that remains of the chitin. This large tube narrows down to a thin elongated neck as it passes through the chitin, and then at its termination bulges out again into an oval swelling (*cap.*) situated always beneath the homogeneous most external layer of chitin. Within this tube is situated a fine chitinous tubule (*ch.t.*) similar to that seen in the branchial sense organs; it lies apparently free in the tube, not straight, but sinuous, and it passes right through all the chitinous layers to open at the surface as a pore; in the last part of its course where it passes

through the most external layer (1) of chitin, it lies always at right angles to the surface.

If the flabellum be stained with methylene blue and with

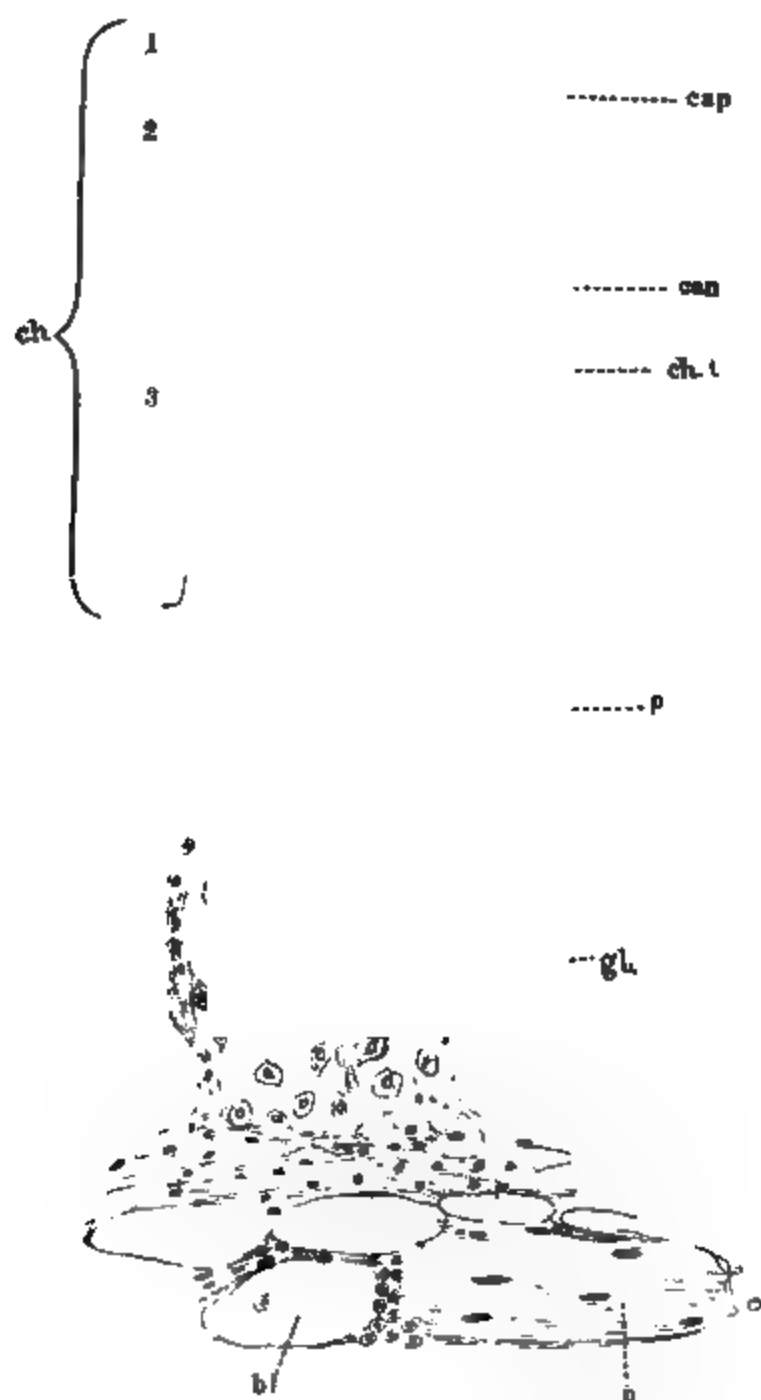


FIG. 5.—Section through three sense organs of flabellum. *bl.*, blood spaces; *n.*, nerve; *gl.*, layer of ganglion cells; *p.*, pigment layer; *ch.* 1, 2, 3, the three layers of chitin; *ch. t.*, chitinous tubule in large tube of sense organ; *cap.*, capitellum or swollen extremity of large tube; *can.*, very fine porous canals or canaliculi of chitin.

acid fuchsin, then all the canaliculi in the chitin show out as fine red lines, and present the appearance given in fig. 5, and it is seen that each of the terminations of the tubules is surrounded in the homogeneous layer of chitin by a thick-set circular patch

of canaliculi, which pass to the very surface of the chitin, while the canaliculi in other parts terminate at the commencement of the homogeneous layer, and do not reach the surface. Further, the contents of the oval swelling, and indeed of the tube as a whole, are stained blue, the chitinous tubule being either unstained or slightly pink in colour. We see, then, that the chitinous tubule alone reaches the surface, while the large tube which contains the tubule terminates in an oval swelling, which often presents a folded or wrinkled appearance as in fig. 6 (see also Patten's fig. 1, Pl. I.). This terminal bulging of the tube is reminiscent of the bulging in the chitinous tubes of the lyriform organs of the Arachnida as described by Gaubert¹ and of the poriferous chordotonal organs in insects as described by Graber² (see fig. 8). This terminal swelling is filled with a homogeneous refringent mass staining blue with methylene blue, in which I have seen no trace of a nucleus; through this the chitinous tubule makes its way without any sign of bulging on its part. Patten, in his description of the sense organs on the mandibles of *Limulus*, which are evidently the same in structure as those on the flabellum, refers to this homogeneous mass as a coagulum. I doubt whether this is an adequate description; it appears to me to take on stains rather more readily than a blood coagulum, yet in the sense of being structureless it resembles a coagulum.

The enormous number of these organs crowded together over the whole flat surface of the flabellum produce a very striking appearance when viewed on the surface. Such a view presents an appearance resembling that of the surface view of the branchial sense organs; in both cases the surface is covered with a great number of closely set circular plaques, in the centre of each of which is seen a well marked pore; the circular plaques in the case of the flabellum are much smaller than those of the branchial sense organs, and clearly are not protrusible as in the latter organs, the appearance of a plaque being due to the ring of thickly set canaliculi round the central

¹ Gaubert, *Recherches sur les organes des sens et sur les systèmes tégumentaire glandulaire et musculaire des appendices des arachnides*, Paris, 1892.

² "Die chordotonalen Sinnesorgane und das Gehör der Insecten," *Archiv. f. mikr. Anat.*, vol. xx. p. 506, 1882.

tubule, as already described. When stained with methylene blue, the surface view of the flabellum under a low power presents an appearance of innumerable circular blue masses, from each of which springs a fine bent hair, terminating in a pore at the surface. The blue masses are the homogeneous substance (*cap.*) of the bulgings seen through the transparent external layer of chitin, and the hairs are the terminal part of the chitinous tubules. Patten has represented the appearance in the mandibles in fig. 2, Pl. I.

- The large tubes in the chitin alter in shape according to their position; those in the middle of the sensory surface of the flabellum, in their course through the chitinous layers, are hardly bent at all; as they approach the two lateral edges of this surface their long thin neck becomes bent more and more, the bending always being directed towards the middle of the surface (see fig. 3); in this way the chitinous tubules increase more or less regularly in length from the centre of the organ to the periphery. The large basal part of the conical tube contains, besides the chitinous tubule, a number of nuclei which are confined to this part of the tube; some of these nuclei look like those belonging to nerve fibres, others are apparently the nuclei of the chitinous membrane lining the tube. I have never seen any sign of nerve cells in the tube itself.

The only other kind of sense organ I have found in connection with these sense organs are a few spike-like projections, the appearance of which is given in fig. 6. I have always seen these in the position given in fig. 3, *sp.*,—*i.e.* at the junction of the surface which contains the sense organs and the surface which is free from them. They are, so far as I have seen, not very numerous; I have not, however, attempted to examine the whole sense organ for the purpose of estimating their number and arrangement.

As is seen in fig. 6, they possess a fine tubule of the same character as that of the neighbouring sense organs, which apparently terminates at the apex of the projecting spike. They appear to belong to the same group as the other poriferous sense organs, and are of special interest, because in their appearance they form a link between these latter and the poriferous sense organs which characterise the pecten of the scorpion (*cf.* fig. 9).

Such, then, is the structure of this remarkable sense organ of the flabellum, as far as I have been able to work it out with the materials at my disposal. It is evident that the flabellar organs, apart from the spike organs, are of the same kind as those described by Patten on the mandibles and chelæ of *Limulus*, and therefore it is most probable that the nerve terminals in the chitinous tubules, and the origin of the latter, are similar in the two sets of organs.

These organs, as Patten has described, are situated in lines on the spines of the mandibles of the prosomatic locomotor appendages, and are grouped closely together to form a compact

Ch. t.

FIG. 6.—Spike organ of flabellum. *ch.t.*, chitinous tubule.

sense organ on the surface of the inner mandible (Lankester's epicoxite) (*im.* in fig. 13), so that a surface view of the organ here gives the characteristic appearance of these poriferous sense patches.

Precisely similar organs are found on the chilaria, which are in function, at all events, simply isolated mandibles (to use Patten's terminology).

On the digging appendage (ectognath), as the comparison of figs. 12 and 13 shows, the mandibular spines are almost non-existent, and the inner mandible or epicoxite is not present, so that the special sense organ of this appendage is represented solely by the flabellum.

This sketch of the special sense organs of *Limulus* shows that all the appendages of *Limulus* possess special sense organs, with the exception of the operculum. All these sense organs are formed on the same plan, in that they possess a fine chitinous tubule passing through the layers of chitin into the underlying hypodermal and nervous tissues, which terminates on the surface in a pore; the surface of the chitin where these pores are situated is perfectly smooth, although in the case of the branchial sense organs the goblet-shaped masses of chitin, each of which contains a pore, are able to be pressed out beyond the level of the surface.

As to their functions, we unfortunately do not know much that is definite. Patten considers that he has evidence of a gustatory function in the case of the mandibular organs, and suggests also a temperature sense in the case of some of these organs. The large organ of the flabellum and the branchial organs he has not taken into consideration; the situation of these organs puts the suggestion of any gustatory function, as far as they are concerned, out of the question, and I do not think it likely that such large specialised organs should be only for estimation of temperature, when one sees how, in the higher mammals, the temperature nerves and the nerves of common sensation are universally distributed over the body. As already stated, the structure of the branchial organs seems to me to point to organs for estimating pressures more than anything else, and I am strongly inclined to look upon the whole set of organs as the derivatives of the lateral sense organs of annelids, such as are described by Eisig in the Capitellidæ. This is Patten's opinion with respect to the mandibular organs; and from what I have shown, these organs cannot be separated in type of structure from those of the flabellum and the branchial sense organs.

In our search, then, for the origin of the vertebrate auditory organ in *Limulus* and its allies, we see so far the following indications:—

1. The auditory organ of the vertebrate is regarded as a special organ belonging to a segmentally arranged set of lateral sense organs, whose original function was co-ordination and equilibration.

2. Such a set of segmentally arranged lateral sense organs is found in annelids in connection with the dorsal cirri of the ventral parapodia.

3. If, as has been supposed, there is a genetic connection between 1 and 2, and if, as I suppose, the vertebrates did not arise from the annelids directly, but from a Protostracan group, then it follows that the lateral sense organs, one of which gave rise to the auditory organ, must have been situated on the Protostracan appendages.

4. In *Limulus*, which is the sole surviving representative of the Palæostracan group, such special sense organs are found on both the prosomatic and mesosomatic appendages, and therefore may be expected to give a direct clue to the origin of the vertebrate auditory organ.

5. Both from its position, its size, and its specialisation, the flabellum, *i.e.* an organ corresponding to the flabellum, must be looked upon as more likely to give a direct clue to the origin of the auditory organ than the sense organs of the branchial appendages, or the gustatory organs of the mandibles.

The Poriferous Auditory Organs of the Arthropoda.

Is there any reason whatever to suppose that poriferous sense organs, such as those of the flabellum, may have given rise to an organ of hearing? In order to answer this question we must first consider whether similar organs are found among Arthropoda; and if so, what their supposed function may be.

There is abundant evidence at the present time, such as that given by Mr and Mrs Packard, to show conclusively that the sense of hearing is present in the Arthropoda; the mere fact of the existence of elaborate stridulating organs is sufficient evidence alone, and it has now been shown that such stridulating organs are not confined to the Insecta, but are present also in the scorpion group. I myself have discovered a distinct stridulating apparatus in various members of the Phrynidæ. This organ forms a well marked oval patch situated on the inner surface of the basal segment of the pedipalp on each side, and is shown in Gaubert's¹ paper; it presents the characteristic appear-

¹ *Op. cit.*, pl. 3, figs. 15, 16.

ance of a stridulating organ, as is seen in fig. 7. The striker of these two organs is apparently the curious appendage-like stylet situated on the prosternite in the middle line, which I have figured in fig. 24, Part VII. of this series of papers¹ (a better figure is given in Blanchard's *L'organisation du Règne Animal*). When the two pedipalps are brought together in the middle line, an oval opening is left between them, into which this stylet



FIG. 7.—A, Stridulating organ on pedipalp of *Phrynosoma* (the markings on the organ are more regular than is shown in the drawing); B, magnified portion of same, showing the absolute regularity of the chitinous ridges.

naturally fits; and seeing that the stylet terminates in two short powerful spikes, which project one at each side, it is evident that it would simultaneously strike the two stridulating organs if the pedipalps were brought together and bent ventrally.

Such seems to me, without doubt, the nature of this organ, and I cannot help thinking Gaubert must be wrong in his views. He paid no attention to the stylet except to mention its existence, and in no way associated it with the organ on the pedipalps.

¹ *This Journal*, vol. xxxiv. p. 558.

This latter organ he describes and figures, and concludes that the two together function as a rasping and comminuting organ for the food before it reaches the mouth,—a suggestion of a most improbable nature when the absolute unfitness of the organ for such a function is considered.

We must, then, take it for granted that Arachnids hear: where is the hearing organ?

Many observers believe that certain surface organs found universally among the spiders, to which Gaubert has given the name of lyriform organs, are auditory in function. His investigations show that they are universally present on the limbs and pro-meso-sternite of all spiders; that they are present singly, not in groups, on the limbs of *Thelyphonus*, and that a group of them exists on the second segment of each limb in the members of the *Phrynus* tribe. In this latter case this organ is the most elaborate of all described by him.

It is especially noticeable that they do not exist in *Galeodes* or in the scorpions, but in the former special sense organs are found in the shape of the so-called racquet organs, on the basal segments of the most posterior pair of appendages, and also, according to Gaubert, on the extremity of the palps and the first pair of feet, while in the latter they occur in the shape of the pectens.

This observation of Gaubert suggests that the place of the lyriform organs in other arachnids is taken in *Galeodes* by the racquet organs and in the scorpions by the pectens. Bertkau, Schimkewitsch, and Wagner, as quoted by Gaubert,¹ all suggest that the lyriform organs of the arachnids belong to the same group of sense organs as the porous chordotonal organs of the *Insecta*, sense organs which have been found in every group of *Insecta*, and are generally regarded as auditory organs. Gaubert does not agree with this, and considers the lyriform organs to be concerned with the temperature sense rather than with audition.

The chordotonal organs of insects have been specially studied by Graber. He divides them into two groups, the poriferous and the non-poriferous, the former being characterised by the presence of pores on the surface arranged in groups or lines. These poriferous chordotonal organs are remarkably constant

¹ *Op. cit.*, pp. 88, 89.

in position, being found only at the base of the wings on the subcostal ridge, in marked contrast to the other group of chordotonal organs which are found chiefly on the appendages in various regions. The striking character of this fixity of position of these organs, and the universality of their presence in the whole group, led Graber to the conclusion that in these poriferous chordotonal organs we are studying a form of auditory apparatus which characterised the ancestor of the insect group. These organs are always well developed on the hind wings, and in the large group of Diptera the auditory apparatus has usurped the whole of the function of the wing; for the balancers, or halteres as they are called, are the sole representatives of the hind wings, and they are usually considered to be of the nature of auditory organs. It is instructive to find that such an auditory organ serves not only for the purpose of audition, but also as an organ of equilibration; thus Lowne¹ gives the evidence of various observers, and confirms it himself, that removal of the balancers destroys the power of orderly flight in the animal. I will not attempt here to discuss the morphological position of the wings of insects, and therefore of this auditory organ, as that would lead too far afield. I am here only concerned with the fact that an auditory organ of a distinct character is present in the thoracic region of all insects, and was almost certainly present in the ancestors of the insects. The surface view of the patch of poriferous organs on the subcostal nervure of the hind wing of *Dytiscus* is represented in fig. 8B, and gives an appearance closely resembling the surface view of the sense organs on the *Limulus* appendages. Like the latter, the sense organ is contained in a wide canal in the chitin (fig. 8A), which broadens at the base, as in the canals of *Limulus*.

Further, a striking peculiarity of these organs in the Insecta as described by Graber is the bulging of the porous canal near its termination (fig. 8C). This bulging is fitted with a homogeneous highly refractive material, from which there passes, according to Lowne,² a chordotonal thread, to be connected with a ganglion cell and nerve. This sphere of refractive material he

¹ *The Anatomy, Physiology, Morphology, and Development of the Blow-fly*, London, 1894 p. 616.

² *Op. cit.*, p. 612.

calls the capitellum of the chordotonal thread. The presence of this material produces upon the surface view an appearance of a halo around the terminal plaque with its central pore; Graber has attempted to represent this by the white area round the central area (in fig. 8B). A very similar appearance is represented by the surface view of the flabellum in those parts where the tube runs straight to the surface, so that the refractive material which fills the oval bulging shines through the overlying chitin, and appears to surround the terminal plaque with a translucent halo.

Such a peculiarity must have a very definite meaning, and



B

FIG. 8 (from Graber).—A, section of subcostal nervure of hind wing of *Dytiscus* to show patch of poriferous organs, *s.o.* B, surface view of poriferous organs; the white space round each organ indicates the deeper lying refringent body which fills the bulging of the canal seen in transverse section in C.

suggests that the canals in the flabellum of *Limulus* and in the hind wings of insects belong to the same class of organ, the chitinous tubule with its nerve terminal in the one case corresponding to the chordotonal thread in the other. One wonders whether this sphere of refractive material or capitellum (to use Lowne's phraseology) is so universally present in order to act as a damper upon the vibrations of the chordotonal thread in the one case or the chitinous tubule in the other, just as the membrana tectoria and the otoliths act in the case of the vertebrate ear.

Patten says that the only organs which seem to him to compare with the gustatory porous organs of *Limulus* are the

sense organs in the extremities of the palps and of the first pair of legs of *Galeodes* as described by Gaubert. I imagine that he was thinking only of arachnids, for the comparison of his drawings with those of Graber show what a strong family resemblance exists between the poriferous sense organs of *Limulus* and those of the insects. On the course of the terminal nerve fibres between the nerve cell and their entrance into the porous chitinous canal, Graber describes the existence of rods or scolophores. On the course of the terminal fibres in the *Limulus* organ between the nerve cells and their entrance into the porous chitinous canal, Patten¹ describes a spindle-shaped swelling, containing a number of rod-like thickenings among the fibrils in the spindle, which present an appearance reminiscent of the rods described by Graber.

It appears as though a type of sense organ characterised by the presence of pores on the surface and a fine chitinous canal which opens at these pores was largely distributed among the Arthropoda. According to Graber, this kind of organ represents a primitive type of sense organ, which was probably concerned with audition and equilibration, and he expresses surprise that similar organs have not been discovered among the Crustacea. It is therefore a matter of great interest to find that so ancient a type of animal as the *Limulus*, closely allied to the primitive Crustacean stock, does possess upon its appendages poriferous sense organs which are directly comparable with these poriferous chordotonal organs of the Insecta.

The Pectens of Scorpions and the Racquet Organs of Galeodes.

The pecten of scorpions must, I think, be considered in connection with this same group of sense organs. The only observer who has described the structure of the sense organs in the pecten is, as far as I know, Gaubert, and he describes their structure together with that of the sense organs of the racquets of *Galeodes*, in connection with the lyriform organs of arachnids, as though he recognised a family resemblance between the three sets of organs.

The pecten of the scorpions is an elaborate sense organ, or

¹ *Op. cit.*, pl. 1, fig. 6.

rather group of sense organs, the special organ being developed on each tooth of the comb; its surface, which is frequently flattened, being directed backwards and inwards, when the axis of the pecten is horizontal at right angles to the length of the body. The surface view of this part of the tooth resembles that of the branchial organs or of the flabellum in *Limulus*, in that it is thickly covered with circular patches, in the centre of



B

C

FIG. 9.—A, section through tooth of pecten of scorpion. *bl.* and *n.*, region of blood spaces and nerves; *gl.*, ganglion cell layer; *ch.*, modified chitinous layer; *s.o.*, sense organ. B, surface view of sense organs. C, goblet of sense organ more highly magnified.

which an ill-defined appearance as of a fine pore is seen. In fig. 9B I give a sketch of the surface view of a part of the organ.

Transverse sections of a tooth of the comb of *Scorpio Europæus* present the appearance given in fig. 9A, and show that each of these circular patches is the surface view of a goblet-shaped chitinous organ, fig. 9C, from the centre of which a short, somewhat cylindrical chitinous spike projects. Within this spike, and running through the goblet into the subjacent tissue, is a

fine tubule. The series of goblets give rise to the appearance of the circular plaques on the surface view, while the spike with its tubule is the reason for the ill-defined appearance of the central pore, just as the terminal pore is much less conspicuous on surface view in the spike organs of the flabellum than in the purely poriferous organs, no part of which projects beyond the level of the chitinous surface.

The fine tubule is soon lost in the thickened but soft modification of the chitinous layer (*ch.*) which is characteristic of the sense organ; at all events, I have not succeeded in tracing it through this layer with any more success than in the corresponding case of the tubules belonging to the smaller goblets of the branchial sense organ of *Limulus* already described.

At the base of the modified chitinous layer a series of cells are seen, many if not all of which belong to the chitinogenous layer. Next to these is the marked layer of ganglion cells (*gl.*), similar to what is seen in the flabellum of *Limulus*. The rest of the space in the section of the tooth is filled up with nerves (*n.*) and blood spaces (*bl.*), just as in the section, fig. 3, of the flabellum of *Limulus*.

Gaubert does not appear to have seen the goblets at all clearly; he describes them simply as conical eminences, and states that they "recouvrent un pore analogue a celui des poils mais plus petit; il est rempli par le protoplasma de la couche hypodermique." From the ganglion there pass, according to him, nervous prolongations which traverse the chitinogenous layer and terminate at the base of the conical eminences. Each of these prolongations "présente sur son trajet, mais un peu plus près du ganglion que de sa terminaison périphérique, une cellule nerveuse fusiforme (*g.*) offrant, comme celles du ganglion, un gros noyau." He illustrates his description with the following fig. 10 taken from his paper.

I have not been able to obtain any evidence of a fusiform nerve cell on the course of the terminal nerve fibres as depicted by him; fusiform cells there are in plenty, as depicted in my drawing, but none with a large nucleus resembling those of the main ganglion. In no case, either in the flabellum or in the branchial organs of *Limulus*, or in the pecten organs, have I ever seen a ganglion cell within the chitin layer; all the nuclei

seen there resemble those of the cells of the hypodermis or else the elongated nuclei characteristic of the presence of nerve fibres. Gaubert's drawing is a striking one, and I have looked through my specimens to see whether there was anything similar, but have hitherto failed in obtaining any definite evidence of anything of the kind.

I feel myself that an exhaustive examination of the structure and function of the pecten of scorpions ought to be undertaken. At present I can only draw the attention of my readers to the similarity of the arrangement of parts, and of the nature of the



FIG. 10 (from Gaubert).—Section of a tooth of pecten of scorpion. *n.*, nerve ; *gl.*, ganglion.

end organs, in the sense organs of the flabellum of *Limulus* and of the pecten of the scorpion. In both cases the special nerve fibres terminate in a massive ganglion, situated just below the chitinogenous layer. In both cases the terminal fibres from these ganglion cells pass through the modified chitinous layer to supply end organs of a striking character ; and although the end organ of the scorpion pecten does not closely resemble the majority of the end organs of the flabellum, yet it does resemble, on the one hand, the isolated poriferous spikes found on the flabellum (fig. 6), and on the other, the poriferous goblets found on the sense patches of the branchial appendages of

Limulus (fig. 1A), so that a combination of these two end organs would give an appearance very closely resembling that of the pecten of the scorpion.

Finally, the special so-called racquet organs of *Galeodes*, which are found on the most basal segments of the last pair of prosomatic appendages, ought also to be considered here. Gaubert has described their structure, and shown how the nerve-trunk in the handle of the racquet splits up into a great number of separate bundles, which spread out fan-shaped to the free edge of the racquet; each of these separate bundles supplies a special sense organ, which terminates as a conical eminence on the floor of a deep groove, running round the whole free edge of the racquet. This groove is almost converted into a canal, owing to the projection of its two sides. Gaubert imagines that the sense organs are pushed forward out of the groove to the exterior by the turgescence of the whole organ; each of the nerve fibres forming a bundle is, according to Gaubert, connected with a nerve cell before it reaches its termination.

This sketch of the special sense organs on the appendages of *Limulus*, of the Scorpions, of *Galeodes* and other Arachnids, and their comparison with the porous chordotonal organs of insects, affords reason for the belief that we are dealing here with a common group of organs, which, although the nature of them is not definitely known, have largely been accredited with the functions of equilibration and audition, a group of organs among which the origin of the auditory organ of vertebrates must be sought for, upon any theory of the origin of vertebrates from arthropods.

Throughout these papers my attention has been especially directed to both *Limulus* and the scorpion group in endeavouring to picture to myself the ancestor of the earliest vertebrates, because the Eurypteridæ possessed such marked scorpion characteristics; so that in considering the origin of a special sense organ, like the vertebrate auditory organ near the junction of the prosoma and mesosoma, it seems to me that the presence of such marked special sense organs as the flabellum on the one hand, and the pecten on the other, must both be taken into account, even although the former is an adjunct to a prosomatic

appendage, while the latter represents, according to present ideas, the whole of a mesosomatic appendage.

From the point of view that the VIIIth nerve represents a segment immediately posterior to that of the VIIth, it is evident that an organ in the situation of the pecten, immediately posterior to the operculum, *i.e.* according to my view, posterior to the segment originally represented by the VIIth nerve, is more correctly situated than an organ like the flabellum, which belongs to a segment anterior to the operculum.

On the other hand, from the point of view of the relationship between the scorpions and the king crabs, it is a possible debatable question whether the pecten really belongs to a segment posterior to the operculum. The position of any nerve in a series depends upon its position of origin in the central nervous system, rather than the position of its peripheral organ. Now Patten¹ gives two figures of the brain of the scorpion built up from serial sections. In both he shows that the main portion of the pectinal nerve arises from a swelling to which he gives the name of *ganglion nodosum*. This swelling arises on each side in close connection with the origin of the most posterior prosomatic appendage nerve, according to his drawings, and posterior to such origin he figures a small nerve (α) which he says supplies the distal parts of the sexual organs. This nerve is the only nerve which can be called the opercular nerve, and apparently arises posteriorly to the main part of the pectinal nerve.

The Origin of the Parachordals and Auditory Cartilaginous Capsule.

In addition to what I have already said, there is another reason why a special sense organ like the pecten is suggestive of the origin of the vertebrate auditory organ, in that such a suggestion gives a clue to the possible origin of the parachordals and auditory cartilaginous capsules.

In the lower vertebrates the auditory organ is characterised by being surrounded with a cartilaginous capsule which springs from a special part of the axial cartilaginous skeleton on each

¹ *Q. J. Micr. Sci.*, vol. xxxi., fig. 1, p. 321, and fig. 4, p. 332.

side known as the pair of parachordals. These latter in *Ammocoetes* form a pair of cartilaginous bars which unite the trabecular bars with the branchial cartilaginous basketwork. They are recognised throughout the *Vertebrata* as distinct from the trabecular bars, thus forming a separate paired cartilaginous element between the trabeculae and the branchial cartilaginous system, which of itself indicates a position for the auditory capsule between the prosomatic trabeculae and the mesosomatic branchial cartilaginous system.

The auditory capsule and parachordals when formed are made of the same kind of cartilage as the trabeculae, *i.e.* of hard cartilage, and are therefore formed from a gelatin-containing tissue, and not from muco-cartilage. Judging from the origin already ascribed to the trabeculae, *viz.*, their formation from the great prosomatic entochondrite or plastron, this would indicate that a second entochondrite existed in the ancestor of the vertebrate in the region of the junction of the prosoma and mesosoma, which was especially connected with the sense organ to which the auditory organ owes its origin.

This pair of entochondrites becoming cartilaginous would give origin to the parachordals, and subsequently to the auditory capsules, their position being such that the nerve to the operculum would be surrounded at its origin by the growth of cartilage.

On this line of argument it is very significant to find that the scorpions do possess a second pair of entochondrites, *viz.*, the supra-pectinal entochondrites which are in special relation with the pectens, so that if the ancestor of the *Cephalaspid* was sufficiently scorpion-like to have possessed a second pair of entochondrites and at the same time a pair of special sense organs of the nature either of the pectens or flabella, then the origin of the auditory apparatus would present no difficulty.

It is also easy to see that the formation of the parachordals from entochondrites homologous with the supra-pectinal entochondrites would give a reason why the VIIth or opercular nerve is involved with the VIIIth in the formation of the auditory capsule, especially if the special sense organ which gave origin to the auditory organ was originally a præ-opercular sense organ like the flabellum which subsequently took up a post-opercular position like that of the pecten.

The Evidence of Ammocetes.

As to the auditory apparatus itself, we see that the elaborate organ for hearing—the cochlea—has been evolved in the vertebrate phylum itself. In the lowest vertebrates the auditory apparatus tends more and more to resolve itself into a simple epithelial sac, the walls of which in places bear auditory hairs projecting into the sac, and in part form otoliths. Such a simple sac forms the early stage of the auditory vesicle in *Ammocoetes*, according to Shipley; subsequently, by a series of folds and growings together, the chambers of the ear of the adult *Petromyzon*, as figured and described by Retzius, are formed. Further, we see that throughout the *Vertebrata* this sac was originally open to the exterior, the auditory vesicle being first an open pit, which forms a vesicle by the coming together of its sides, the last part to close being known as the *recessus labyrinthicus*; in many cases, as in *Elasmobranchs*, this part remains open, or communicates with the exterior by means of the *ductus endolymphaticus*.

Judging, therefore, from the embryological evidence, it would appear that the auditory organ originated as a special sense organ formed by modified epithelial cells of the surface, which epithelial surface becoming invaginated, came to line a closed auditory vesicle under the surface. This special sense organ was innervated from a large ganglionic mass of nerve cells, situated close against the peripheral sense cells, the axis-cylinder processes of which formed the sensory roots of the nerve.

Yet another peculiarity of striking significance is seen in connection with the auditory organ of *Ammocoetes*. The opening of the cartilaginous capsule towards the brain is a large one (fig. 11), and admits the passage not only of the auditory and facial nerves, but also of a portion of the peculiar tissue which surrounds the brain. The large cells of this tissue, with their poorly staining nucleus and the pigment between them, make them quite unmistakeable; and, as I have already stated, nowhere else in the whole of *Ammocoetes* is such a tissue found. When I first noticed these cells within the

auditory capsule, it seemed to me almost impossible that my interpretation of them as the remnant of the generative and liver tissue which surrounds the brain of animals like *Limulus* could be true, for it seemed too unlikely that a part of the generative system could ever have become included in the auditory capsule. Still they are undoubtedly there; and, as already argued with respect to the substance round the brain, they must represent some pre-existing tissue which was functional in the ancestor of *Ammocoetes*. If my interpretation was right, this tissue must be generative and liver tissue, and its



FIG. 11.—Transverse section through auditory capsules and brain of *Ammocoetes*. *Au.*, auditory organ; VIII, auditory nerve; *gl.*, ganglion cells of VIIIth nerve; *Au.cart.*, cartilaginous auditory capsule; *gen.*, cells of old generative tissue round brain and in auditory capsule; *bl.*, blood-vessels.

presence in the auditory capsule immediately becomes a most important piece of evidence, for it proves that the auditory organ must have been originally so situated that a portion of the generative and liver mass surrounding the cephalic region of the nervous system followed the auditory nerve to the peripheral sense organ.

Here there was a test of the truth of my theory ranking second only to the test of the median eyes; the strongest possible evidence of the truth of any theory is given when by its aid new and unexpected facts are brought to light. The

theory said that in the group of animals from which the Vertebrates arose a special sense organ of the nature of an auditory organ must have existed on the base of one of the appendages situated at the junction of the prosoma and mesosoma, and that into this basal part of the appendage a portion of the cephalic mass of generative and liver material must have made its way in close contiguity to the nerve of the special organ.

The only living example which nearly approaches the ancient extinct forms from which, according to the theory, the vertebrates arose, is *Limulus*, and, as has already been shown, in this animal, in the very position postulated by the theory, a large special sense organ—the flabellum—exists, which, as described in this paper, may well have given rise to a sense organ concerned with equilibration and audition. If, further, it be found that a diverticulum of the generative and liver material does accompany the nerve of the flabellum into the basal part of the appendage, then the evidence becomes very strong that the auditory organ of *Ammocoetes*, *i.e.* of the ancient Cephalaspids, was derived from an organ homologous with the flabellum; that, therefore, the material round the brain of *Ammocoetes* was originally generative and liver material; that, in fact, the whole theory is true, for all the parts of it hang together so closely that if one portion is accepted, all the rest must follow. As pointed out in my address at Liverpool, and at the meeting of the Philosophical Society at Cambridge,¹ it is a most striking fact that a mass of the generative and liver tissue does accompany the flabellar nerve into the basal part of this appendage. Into no other appendage of *Limulus* is there the slightest sign of any protrusion of the generative and liver masses; nowhere except in the auditory capsule is there any sign of the peculiar large celled tissue which surrounds the brain and upper part of the spinal cord of *Ammocoetes*. The actual position of the flabellum on the basal part of the ectognath is shown in fig. 12A, and in fig. 12B I have removed the chitin to show the generative and liver tissue (*gen.*) lying beneath.

The reason why to all appearance only the generative and liver mass penetrates into the basal part of this appendage is

¹ *Proc. Cambridge Philos. Soc.*, vol. ix. p. 19, 1895.

apparent when we see (as Patten and Redenbaugh have pointed out) to what part of the appendage the flabellum in reality belongs.

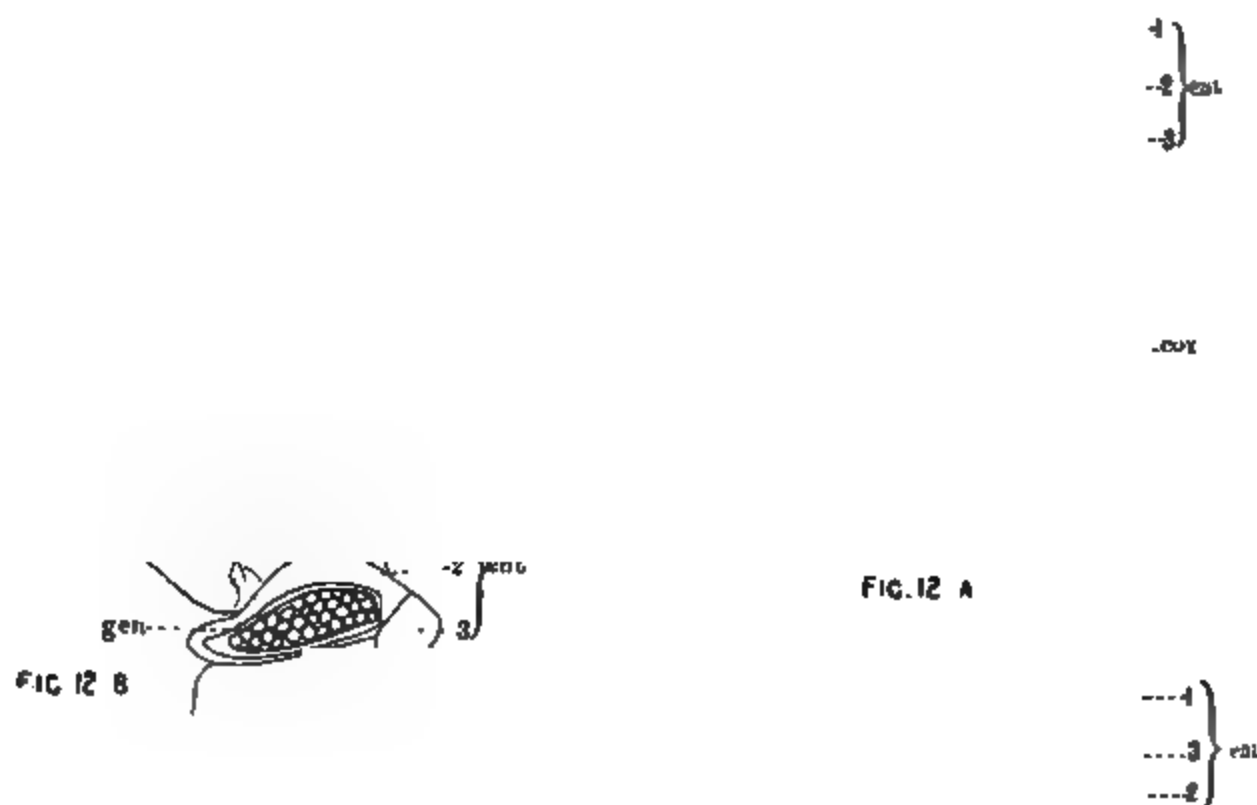


FIG. 12.—A, the digging appendage or ectognath of *Limulus*. *cox.*, coxopodite; *ent.*, entocoxite; *fl.*, flabellum. B, the middle protuberance (2) of the entocoxite opened, to show the generative and liver tissue (*gen.*) within it.

FIG. 13.—One of the prosomatic locomotor appendages or endognaths of *Limulus*, for comparison with fig. 12. *cox.*, coxopodite; *ent.*, entocoxite; *m.*, mandible; *i.m.*, inner mandible or epicoxite.

(For the drawing of these two figures and of fig. 2, I am indebted to Miss R. Alcock.)

Patten and Redenbaugh,¹ in their description of the prosomatic appendages of *Limulus*, describe the segments of the limbs as (1)

¹ "Studies on *Limulus*.—II. The nervous system of *Limulus Polyphemus*," *Jour. of Morph.*, vol. xvi. p. 91.

the dactylopodite, (2) the propodite, (3) the mero- and carpopodites, (4) the ischiopodite, (5) the basipodite, and (6) the coxopodite (*cox.* in figs. 12 and 13). Still more basal than the coxopodite is situated the entocoxite (*ent.* in figs. 12 and 13), which is composed of three sclerites or sensory knobs, to use Patten's description. The middle one of these three sclerites (2 in fig. 13) enlarges greatly in the digging appendage, and grows over the coxopodite (2 in fig. 12) to form the base from which the flabellum springs. Thus, as they have pointed out, the flabellum does not belong to the coxopodite of the appendage, but to the middle sensory knob of the entocoxite. Upon opening the prosomatic carapace it is seen that the cephalic generative and liver masses press close against the internal surface of the prosomatic carapace and also of the entocoxite, so that any enlargement of one of the sensory knobs of the entocoxite would necessarily be filled with a protrusion of the generative and liver masses. This is the reason why the generative and liver material apparently passes into the basal segment of the ectognath, and not into that of the endognaths; it does not really pass into the coxopodite of the appendage, but into an enlarged portion of the entocoxite, which can hardly be considered as truly belonging to the appendage. Kishinouye¹ has stated that a knob arises in the embryo at the base of each of the prosomatic locomotor appendages, but that this knob develops only in the last or digging appendage (ectognath) forming the flabellum. Doubtless the median sclerites of the entocoxites of the endognaths represent Kishinouye's undeveloped knobs.

I would conclude, then, that the flabellum, together with its basal part, is an adjunct to the appendage rather than a part of it, and might therefore easily remain a separate and well developed entity, even although the appendage itself dwindled down to a mere tentacle.

To sum up. The evidence appears to me very strong that the flabellum of *Limulus* and the pecten of Scorpions are the most likely organs to give a clue to the origin of the auditory apparatus of Vertebrates. At present both the Eurypterids and

¹ "On the development of *Limulus Longispina*," *Jour. of Coll. of Sci., Imp. Univ. Japan*, vol. v., 1891.

Cephalaspids have left us in the lurch: in the former there is no sign of either flabellum or pecten; in the latter, no sign of any auditory capsule beyond Rohon's¹ discovery of two small apertures situated dorsally on each side of the middle line in *Tremataspis*, which he considers to be the termination of the *ductus endolymphaticus* on each side. In both cases it is probable, one may almost say certain, that any such special sense organ, if present, was not situated externally, but was sunk below the surface as in *Ammocoetes*.

The method by which such a sense organ situated externally on the surface of the animal comes phylogenetically to form the lining wall of an internally situated membranous capsule is given by the ontogeny of this capsule, which shows step by step how the sense organ sinks in and forms a capsule, and finally is entirely removed from the surface, except for the *ductus endolymphaticus*.

In concluding this sketch of the manner in which the auditory apparatus, in accordance with the rest of my theory, may have arisen, I feel strongly the number of gaps in the chain of evidence. I have felt, however, that the filling up of those gaps, *e.g.* the systematic investigation of the functions of the flabellum and pecten, would take a large amount of time, and necessitate residence out of England for a time; and as I desire to put before my readers my views as to the origin of all the organs of *Ammocoetes*, and not only those connected with the cranial nerves, I feel that it is better now to pass on to the spinal region rather than to spend time at present working out points connected with the auditory nerve more fully than is given in this paper.

I will therefore in this paper conclude what I have to say on the cranial nerves; and, in accordance with my promise, summarise the previous chapters by briefly considering the origin of the cranial nerves as given by my theory in the light of the principles laid down in Part I. of this series of papers.

SUMMARY OF THE ORIGIN OF THE CRANIAL NERVES.

The starting-point of the whole of my theory of the origin of Vertebrates was my paper on the manner in which the cranial

¹ *Mem. Acad. St. Petersburg.*, vol. 38, No. 13, 1892.

nerves are built up, which led me directly to the conclusion that the segmental nerves of the ancestor of the vertebrate must have been originally composed of three roots, not two as in the spinal, viz., (1) a sensory nerve to the integument, (2) a mixed sensory and motor nerve to the splanchnic segment, and (3) an essentially motor nerve to the somatic muscles,—although this latter might contain as well the sensory nerves of those muscles; so that by combining the first and third we might speak of the cranial nerves as possessing not dorsal sensory and ventral motor roots, but rather mixed roots to splanchnic and somatic segments. As mentioned, the researches of Milne Edwards on the arrangement of the nerves of *Limulus* showed that a similar triple arrangement of nerve roots was present in that animal, for each ganglion gave off (1) sensory nerves to the integument, which he called epimeral nerves, (2) mixed motor and sensory nerves to the appendage, and (3) short nerves to the neighbouring body muscles. Applying Milne Edwards' investigations to elucidate the origin of the cranial nerves of vertebrates, I concluded that the appendage nerve gave origin to the nerve to the splanchnic segment, and that therefore the Xth, IXth, VIIth, and Vth (in part) nerves were originally nerves to appendages, while the ascending root of the Vth represented the epimeral or integumentary sensory nerves, and the IIIrd, IVth, and VIth nerves the motor somatic nerves. Further, I concluded that the eye muscles supplied by these latter did not belong to the longitudinal muscles of the body, but to the dorso-ventral group, those markedly segmental muscles which are so characteristic of the *Limulus* and Scorpion group of animals. In order that the arrangement in *Limulus* should harmonise with that of the vertebrate, it ought to be proved definitely that the dorso-ventral muscles are supplied by Milne Edwards'¹ third nerve root, for although the probability is great that he included them in his term 'neighbouring muscles,' yet he does not definitely state their nerve supply. I wish, therefore, to take this opportunity of pointing out that Patten and Redenbaugh, in their recent paper² on the nerves of *Limulus*, have shown that these very nerves do supply the dorso-ventral body muscles as well as the longitudinal body

¹ *Anatomie des Limules.*² *Op. cit.*

muscles, the two arising from the ganglion separately, but both included in Milne Edwards' third group (*cf.* Patten and Redenbaugh, fig. 6, Pl. IX.). Patten and Redenbaugh call them intestinal nerves, because they have traced fibres from them to the intestine, which Milne Edwards did not do. They are undoubtedly the motor nerves to the longitudinal and dorso-ventral body muscles, whether or no they supply the intestine as well.

PRINCIPLE 1.—In assuming variations to arise in an ancestor, the amount of change assumed, and its direction, must agree with the kind of variation known to exist in the various members of the group to which the ancestor belongs, and the amount of variation assumed should be limited.

The variations which I have assumed to have taken place have resulted in the conversion of the mesosomatic and prosomatic appendages of the arthropod into the splanchnic segments of the vertebrate, and consist essentially of two processes, viz., the inclusion of the mesosomatic appendages into the body of the animal, with the formation of a respiratory chamber, and the dwindling of the foremost prosomatic appendages within an oral chamber, together with the growth and extension of the last pair of prosomatic appendages. Both these variations are the great characteristic of the group of the Palæostraca to which the ancestor is supposed to belong, and the amount of variation assumed is no more than what is known to occur in that group.

Thus we see that the great characteristic of the group of scorpions is the inclusion of the free mesosomatic branchial appendages into the body of the animal, with the result that all appearance of appendages is gone, and only branchiæ are left, and we find in forms like *Thelyphonus* that a common chamber has already been formed for the foremost pair of branchiæ. The change required to form the respiratory chamber of *Aminocætes* from a series of paired respiratory appendages similar to the foremost pair in *Thelyphonus* is no greater, if as great, as the change

required to pass from the free branchial appendages of *Limulus* to the closed lung books of *Scorpio* or the gills of *Eurypterus*.

As to the prosomatic appendages, the variation assumed consists in the formation of short tactile tentacles from what were originally prehensile masticating appendages, and the formation of the lower lip from the last pair of prosomatic appendages. Both these variations are the natural sequence of a continuance of the changes already seen in the group; the same process which has transformed the powerful chelate locomotor appendages like those of *Limulus* into the small tactile appendages of *Eurypterus* and *Drepanopterus*, and the abortive chilaria of *Limulus* into the massive metastoma of *Pterygotus* or *Slimonium*, would, if continued, result in the formation of tentacles and a lower lip similar to that of *Ammocoetes*.

The variation assumed to account for the eye muscles of vertebrates and their nerves is a simple movement of the lateral eyes nearer the mid-dorsal line, in consequence of which the dorso-ventral prosomatic body muscles were able to be utilised as movers of the eye. Such a variation is strictly in conformity with what is found in the group.

The variation assumed to account for the peculiarities of the lateral eyes of vertebrates is a closer connection of these eyes with two anterior diverticula of the old cephalic stomach, a variation which is simply a continuation of what is already seen in its commencement in certain primitive members of the group.

The formation of the vertebrate auditory apparatus is assumed to have arisen by the sinking in of a superficial sense organ so as to form a vesicle. Such a method of formation is frequently found in the Arthropoda, as is seen in the auditory organ of *Astacus*, etc.

The formation of the olfactory organ is a direct consequence of the variation which has already occurred in the group, viz., the transformation of the paired olfactory antennæ of the crustacean into the median camerostome of the scorpions.

PRINCIPLE 2.—The kind of variation by which members of the higher group have steadily risen from the lowest to the highest forms must be in accordance with the supposed variations by means of which the lower group has approximated to the higher.

The marked variation in the lower group is the reduction of the appendages, and the attainment thereby of a smooth, lithe body surface, by which a crawling, semi-swimming animal like *Limulus* was converted into a free-swimming animal like *Eurypterus*.

The conversion of the arthropod into the fish is the conversion of a crawling into a swimming animal, with the same result as has occurred in the whale, viz., the dwindling and inclusion of all sticking-out appendages except those which have become utilised, as in the conversion of the prosomatic appendages of *Ammocoetes* into the suctorial apparatus of *Petromyzon*,—a change which is especially reminiscent of the nature of the lower group.

When we compare the earliest fishes with the later ones, we see how the members of the *Pteraspidae*, *Cephalaspidae*, and *Antiarcha* possessed but little mobility in comparison with the fishes of a later age. The whole onward progress was towards a greater elongation and flexibility of body, combined with a less heavily weighted head region, so as to produce a more and more efficient swimming machine.

PRINCIPLE 3.—Changes of function can arise when the new function coexists, perhaps subordinately, with the primary function ; or coexists in another member of the same group, or in one of its larval forms.

The function of the various appendages, upon my theory, remains the same in the vertebrate as in the arthropod. Thus the olfactory appendages still subserve the functions of smell, the auditory apparatus is still concerned with equilibration and co-ordination of movements, the prosomatic appendages still take part in mastication and act as sensitive tactile organs, while the mesosomatic appendages still subserve the function of

respiration. In connection, however, with the latter, a new function has become prominent, viz., that of digestion, and doubtless in the minds of many this digestive power is a flagrant violation of Principle 3. After Miss Alcock's paper¹ all such difficulty is removed, for we see that the power of proteid digestion is already possessed by the secretion of the epidermal cells of various arthropods for the purpose of keeping the surface clean, so that it would follow quite naturally that such cells coming to form the lining of a respiratory chamber, should still continue to function as digestive cells.

The only other instance of a possible change of function in any of the assumed appendages is that of the opercular or thyroid appendage, where a glandular organ in connection with the sexual organs of the arthropod is assumed to have become the thyroid gland. As far as the actual function of the thyroid gland as a ductless gland is concerned, its regulation of the amount of iodine in the body, it is impossible to say whether or no any similar function was possessed by the uterine glands of the old sea scorpions and their allies; the striking discrepancy consists rather in the fact that the one organ was closely connected with sexual functions, while the other is far removed from the genital organs, and *a priori* would never be thought to have any connection with such functions.

Yet it is a strange fact that Freund² has shown, and shown conclusively, that there is an intimate connection between the condition of the thyroid gland and the state of the sexual organs, not only in human beings, but also in numerous animals such as dogs, sheep, goats, pigs, and deer. He points out that the swelling of the gland which occurs in consequence of sexual excitement (a fact mentioned both in folk-lore tales and in poetical literature), and also the swelling at time of puberty, may both lead to a true goitrous enlargement; that most of the permanent goitres commence during a menstrual period; that during pregnancy swelling of the thyroid is almost universal, and may attain so large a size as to threaten suffocation or even cause death; that

¹ "On Proteid Digestion in *Ammocoetes*," *this Journal*, vol. xxxiii. p. 612.

² Freund, "Die Beziehungen der Schilddrüse zu den weiblichen Geschlechts Organen," *Deutsche Zeitsch. f. Chirurgie*, Bd. 18, p. 213, 1883.

the period of puberty and the climacteric period are the two maximal periods for the onset of goitre.

Most marked is the evidence of exophthalmic goitre, in which, according to Freund, the undoubted causes are (1) the hysterical nervous constitution, and (2) sexual excess. In most cases he finds an actual inflammatory condition of the *parametrium*, i.e. the pelvic cellular tissue which surrounds the cervix of the uterus, so that he declares that the most striking and evident cause of exophthalmic goitre in women is the disease called *parametritis chronica atrophicans*.

This unexpected sympathy between the thyroid gland and the sexual organs, leading even to disease, is unaccountable and most improbable if the thyroid is simply a gland connected with the alimentary canal, but most suggestive, and indeed probable, if the thyroid, as I have suggested, was once a portion of the sexual apparatus.

It may perhaps be argued that a change of function has taken place in the olfactory tube and in the optic diverticula in consequence of the assumed closure of the old mouth; in the former case the olfactory function was there when the old mouth was still functional; all that is assumed to have happened is that food no longer passes along the olfactory passage or nasal tube, as it has now become, and it is therefore entirely confined to its proper function of smelling. In the latter case the anterior diverticula were nutrient tubes to the brain region before the closure of the old mouth, and in the vertebrate, as long as they are patent, the optic diverticula in all probability bring nutrient fluid to the nervous tissues of the eye.

PRINCIPLE 4.—Organs which are clearly rudimentary in the higher group must be derived from corresponding organs which are functional in the lower.

This principle is thoroughly borne out in the consideration of all organs that can be called rudimentary in connection with the presumed appendages. We have especially to consider the thyroid gland, the tubular muscles of *Ammocoetes*, and the pituitary body. The very presence of these rudimentary organs in *Ammocoetes*, and the manner in which their presence

is explained upon examination of the special invertebrate group, is the strongest argument in favour of my theory. I have already discussed the pineal eyes and the rudimentary tissue around the brain in connection with this principle, and will only add that the consideration of the auditory organ has confirmed and strengthened the interpretation given, that this peculiar tissue owes its origin to the mass of generative and so-called liver tissue which surrounds the brain, and passes in to the base of the flabellum of such an animal as *Limulus*. The thyroid gland of vertebrates may be in a sense included in rudimentary organs, when we see how it arises in *Petromyzon* from the partial destruction of the much more elaborate organ of the *Ammocoetes*. It is this latter organ which was derived directly from the glandular organs of the terminal genital duct situated on the median tongue of the operculum in the ancient Palæostracan forms.

The tubular muscles may be classed among rudimentary organs, because they form a very well marked system in *Ammocoetes*, and entirely disappear at transformation; I¹ have explained their existence in *Ammocoetes* by the suggestion that they represent the veno-pericardial system of muscles which are so characteristic of the *Limulus* and Scorpion groups. In my paper I stated that if this suggestion were true, then the innervation of the veno-pericardial muscles in *Limulus* ought to bear witness to its truth, and such witness ought to be of a very striking character, for Miss Alcock² had shown that the innervation of the tubular muscles in *Ammocoetes* is very peculiar and unexpected, and therefore, if a similar peculiarity was found in the arrangement of the nerves in *Limulus*, it would form the strongest possible proof, not only of the correctness of my explanation of the existence of the tubular muscles in *Ammocoetes*, but also of my whole theory, which, step by step, had led up to such an explanation. Even while I wrote, confirmatory and most suggestive evidence had been published, for Patten and Redenbaugh had just brought out their great paper on the nerves of *Limulus*, but I did not see it until after my paper had left my hands.

¹ Part VII. of this series of papers, *this Journal*, vol. xxxiv. p. 550.

² *This Journal*, vol. xxxii., 1898.

Miss Alcock has shown that the segmental tubular muscles of *Ammocoetes* are innervated, not by the branchial nerves of each segment, but by the *profundus branchialis* branch of the VIIth nerve, with the exception of the tubular muscles of the velum, which are innervated by the velar nerve from the Vth, a nerve which supplies the muscles of the lower lip. Now, according to my theory, the VIIth nerve originally supplied the operculum, and the lower lip nerve was the nerve to the metastoma, *i.e.*, in *Limulus* to the chilarium, and the tubular muscles were the veno-pericardial muscles; so that Miss Alcock's discovery asserted this apparently very improbable prophecy, that in an animal like *Limulus* a nerve ought to arise from the 7th and 8th neuromeres belonging to the chilarial and opercular segments, which, instead of being confined to those segments, should traverse the whole branchial region on each side, giving off a branch to each branchial segment, and that this branch should supply the veno-pericardial muscle of that side.

Patten and Redenbaugh, in their paper, describe how the cardiac segmental nerves arise from each neuromere to join the median nerve of the heart, all segmental, all arranged on the same plan, with the exception of the cardiac nerves of the chilarial and opercular neuromeres. To quote their words in their summing up,¹ "The cardiac nerves of the chilarial and opercular neuromeres are completely fused, and on the hæmal (dorsal) side of the body form the pericardial nerve, which extends into the five branchial neuromeres," and, as they state, gives a branch to each of the cardiac nerves of the branchial neuromeres.

This observation of Patten and Redenbaugh shows that the pericardial nerve of *Limulus* agrees with the very nerve postulated by the theory, as far as concerns its origin from the chilarian and opercular neuromeres, its remarkable course along the whole branchial region, and its segmental branches to each branchial segment. It only remains, in order to make the prophecy complete, to show that these segmental branchial branches supply the system of veno-pericardial muscles.

I have therefore cut a series of sections through the veno-

¹ *Op. cit.*, p. 178.

pericardial muscles to see whether their nerve supply enters the muscle from the longitudinal venous sinus end or the pericardial end of the muscle, and have found that a well defined nerve enters in at the venous sinus end of the muscle, and not at the pericardial end, so that there is no direct branch from the pericardial nerve to the veno-pericardial muscle. Still there is, as Patten and Redenbaugh describe, a branch given off by the pericardial nerve to each segmental cardiac nerve, and that branch must reach the periphery somewhere; it may perfectly well travel along with the segmental cardiac nerve, even right up to the ganglion, and then leave it to supply the veno-pericardial muscle at the venous sinus end. Whether that is so or not can only be settled by the direct experiment of stimulating the pericardial nerve or its branch in the living animal, and is not possible to settle by anatomical methods which alone are available to me in England.

PRINCIPLE 6.—Any explanation of the origin of a higher group from a lower group must be confirmed by the study of the development in the higher group.

The explanation in question asserts that the splanchnic segmentation of the vertebrate is derived from the appendages of the arthropod. This principle therefore demands that the splanchnic segments should arise in the vertebrate after the fashion of appendages, in other words, as a series of out-bud-dings from the surface, which in the case of sunk-in appendages would take the form of in-buddings into the body. Embryology, on the other hand, asserts that the splanchnic segments are formed by the formation of visceral pouches, and that the oral cavity is formed by an invagination called the stomodæal invagination, in other words, a series of invaginations, and evaginations characterise the formation of the splanchnic segments and the oral cavity of the vertebrate. There is, then, here an apparent discrepancy; the vertebrate, according to this view, does not in its development show the presence of former appendages, but of pouches.

Let us look at this matter a little closer; it is perfectly clear that an invagination or a pouch may be formed in two ways:

(1) by the pushing in or thinning down of a circumscribed surface area; (2) by the out-budding or forward growth of the parts surrounding that surface area.

By the second method we see that a series of so-called evaginations or pouches would really be a sign of a series of in-buddings or appendages, the spaces between which would form the pouches.

Let us consider, first, the so-called stomodæal invagination of *Ammocoetes*; as already mentioned,¹ the pictures given by Dohrn and Kupffer point directly to the conclusion that this chamber is really formed by the forward growth of the upper and lower lips, while undoubtedly the tentacular appendages are formed as out-buddings within this chamber. As far, then, as these prosomatic appendages are concerned, they are formed after the fashion of arthropod appendages.

Next consider the mesosomatic or branchial appendages. If each one of the so-called diaphragms originated, as I suppose, from a branchial appendage, each gill pouch being simply the portion of the respiratory chamber between two branchial appendages, then the development ought to show that the diaphragms are formed by marked ingrowths taking place at intervals; while, on the other hand, if the formation of pouches in a uniform chamber is the characteristic of the vertebrate branchial formation, then the ontogeny ought to show rather a thinning-down process in a uniform thick wall, which, taking place at regular intervals, leads to the formation of pouches, which ultimately break through as gill slits.

The evidence of Shipley and Dohrn² is distinctly in favour of the formation of the diaphragms as a marked ingrowth of tissue at definite intervals, just as would be the case if they represented appendages budding into a common chamber. Thus Shipley³ says, "The gill slits appear to me to be the result of the ventral downgrowths of mesoblast taking place only at certain places, these forming the gill bars. Between each downgrowth the hypoblastic lining of the alimentary canal remains in contact with the epiblast, and here the gill opening subsequently appears

¹ Part VII. of this series of papers, *this Journal*, vol. xxxiv. p. 539.

² *Stud. z. Urgeschichte des Wirbelthierkörpers*, No. xiii. taf. 10, figs. 6-16.

³ *Q. J. Micr. Sci.*, 1887, p. 24.

about the twenty-second day." Dohrn in his pictures demonstrates the rapid increase of the in-building by which the diaphragms are formed. His pictures clearly show that these respiratory diaphragms are formed just as they would be formed if they represented a series of ingrowing branchial appendages.

The developmental evidence is to my mind perfectly consistent with the idea that the branchial unit is the tissue between the pouches,—represented by each of the splanchnic mesoblastic segments,—in other words, a branchial appendage. The difficulty does not arise in connection with this conception, but rather with the interpretation of the cavity into which these branchial appendages depend; the formation, in fact, of the respiratory or pharyngeal chamber. This chamber is, if I understand rightly, considered to be developed from the most anterior portion of the archenteron, so that its consideration from a developmental point of view cannot be separated from the consideration of the so-called gastrulation of the vertebrate, a chapter in this history which I hope to discuss shortly.

Between the respiratory and oral chambers ontogeny shows that a septum originally existed, which by breaking through allowed the oral chamber to communicate with the respiratory chamber; this, according to the theory, is a direct indication in the ontogeny of what occurred in the phylogeny.

When this septum was intact, then the hypophysial tube was ventral; then the tentacles were at their largest, in comparison to the size of the animal; then the upper lip had not begun its forward development, by means of which the nasal orifice became dorsal; so marked is this period of the animal's development, so rapid is the transformation to the Ammocetes stage, that Kupffer designates it the larval stage of Ammocetes, just as by a subsequent transformation the Ammocetes form or larval stage of Petromyzon gives rise to the adult Petromyzon.

In the larval stage of Ammocetes the whole configuration of the head of the animal can be compared to a Palæostracan form; after this stage, when the Ammocetes is formed, then the configuration becomes Cephalaspid rather than Eurypterid.

Further, the formation of the coelomic cavities in the cranial region and the formation of the eye muscles is a strong con-

firmation from the developmental side of the truth of the theory.

It seems to me, I must confess, that if we consider the formation of the organs of the head region of *Ammocoetes* simply as organs, without troubling as to whether they are derived from this or that germinal layer, it is difficult to see how ontogeny could be expected to indicate the phylogenetic evolution more clearly than it does do in the case of *Ammocoetes*. Of course the difficulty of the notochord remains, and cannot be considered until I deal with the vertebrate alimentary canal as a whole, *i.e.*, until after the spinal region has been considered as well as the cranial; still, assuming that an explanation of the notochord is possible, and simply taking the origin of the cranial nerves as put forward in these first ten parts of this series of papers, it seems to me that not only is the embryological evidence in accordance with the theory elaborated, but itself has again and again indicated the manner in which the passage from the *Palæostracan* to the *Cephalaspid* took place in *Palæozoic* times.

Journal of Anatomy and Physiology.

ON THE DEVELOPMENT OF THE HEAD MUSCLES IN THE NEWT. By F. H. EDGEWORTH, M.B., B.Sc., *Assistant Physician to the Bristol Royal Infirmary.*

(From Prof. Fawcett's Laboratory, Bristol Medical School.)

IN an article published two years ago in *this Journal*¹ the formation of the muscles, other than those of the eyes, in the head of the toad was traced. They were shown to develop from successive dorso-ventrally placed solid strips of aggregated mesoblast cells on either side of the anterior portion of the alimentary canal. And reasons were put forward for holding that the dorsal portions (and the muscles into which they develop) represent somatic, and the ventral portions splanchnic, structures. There was, however, no definite proof, as, unlike what obtains in Elasmobranchs, the mesoblast strips are solid from the first, and do not contain any sections of the body cavity.

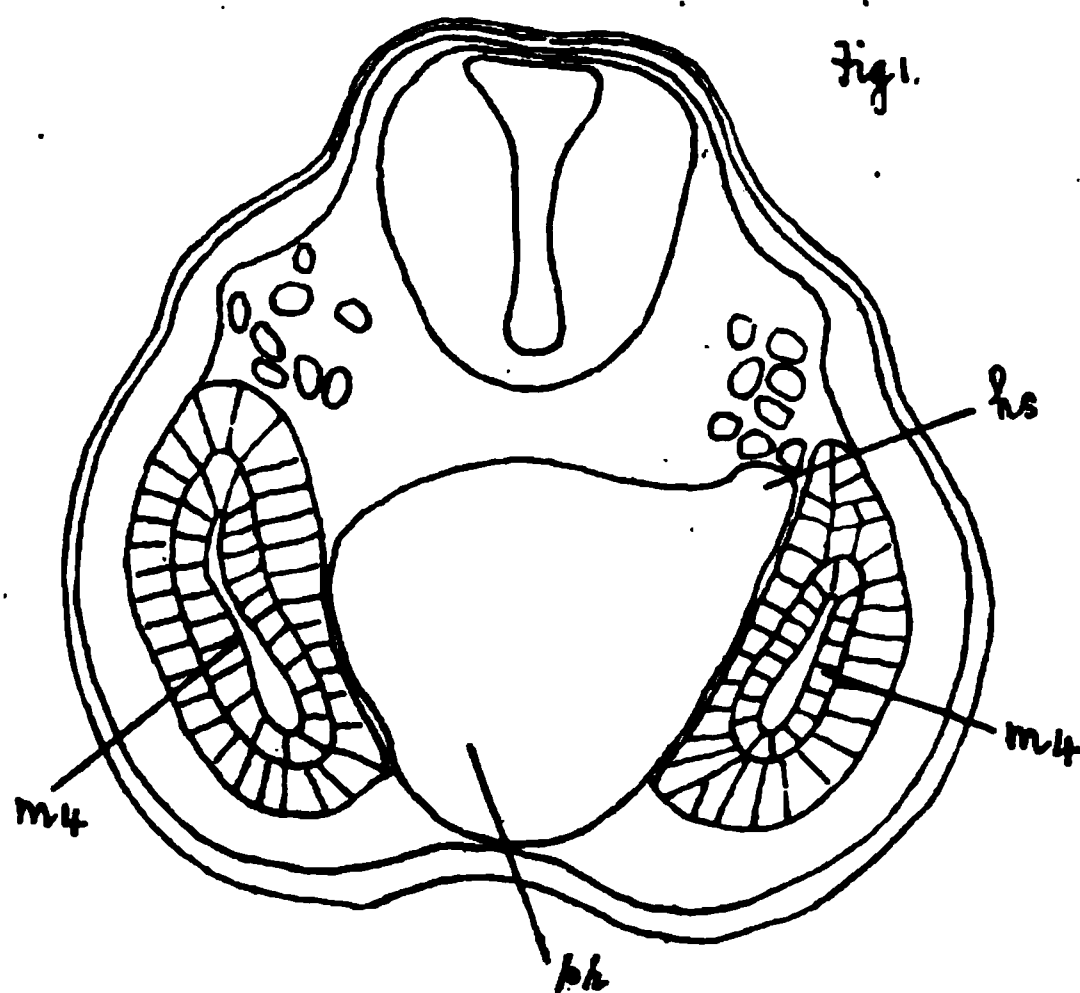
It seemed, then, that it would be of some interest to investigate the development of the head muscles in the Newt, for Scott and Osborn² showed many years ago that the early condition of the mesoblast in the head of that animal is exactly comparable with that of Elasmobranchs. They state that the mesoblast of the head is formed by forward growth from the body region, and on either side forms at first a solid plate. In this a split appears, the pleuro-peritoneal cavity, which becomes continuous with the later formed portion of that cavity in the trunk. The first visceral cleft divides the mesoblast into two

¹ Vol. xxxiv. p. 113 ff.

² "On the early development of the common Newt," *Quart. Jour. Micr. Sci.*, vol. xix., 1879.

portions, one in front and the other behind; the second cleft divides the hinder portion into two, and so on. The section in front of the first cleft divides into two, one portion remaining altogether enclosed in the mandibular arch, whilst the other lies close to the optic vesicle. The later development was not followed out. Scott and Osborn end by stating that "in the posterior part of the head there are four segments which give rise to muscular fibres as in *Bombinator*, and continue the dorsal muscle forward."

Since this paper, the only one published, as far as I know,



dealing with the head of the newt, is that by Miss Alice Johnson, and Miss Lilian Sheldon.¹ In this, among other things, the early development of the cranial nerves is described, but that of the muscles is not touched on.

In the following paper the development of the muscles in the maxillary, hyoid, and branchial segments is traced from the latest stage described by Scott and Osborn, up to that in which the newt is 24 mm. long, with well developed front and hind legs.

Embryos of the crested newt (*Triton cristatus*) were fixed in Gilson's mixture, hardened in alcohol, cut out (when necessary)

¹ "Notes on the early development of the Newt," *Q.J.M.S.*, vol. xxvi.

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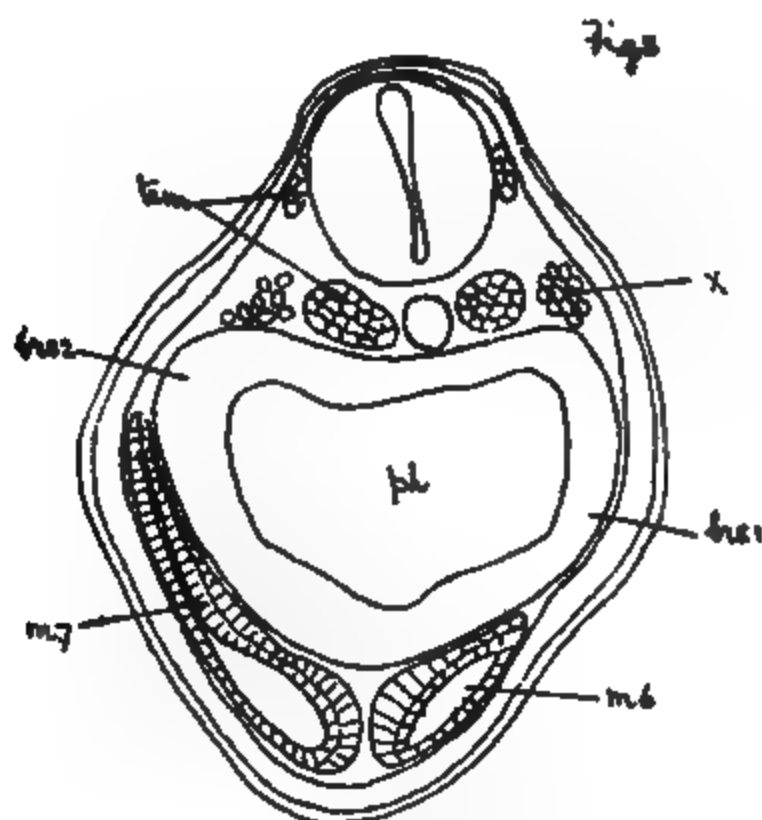
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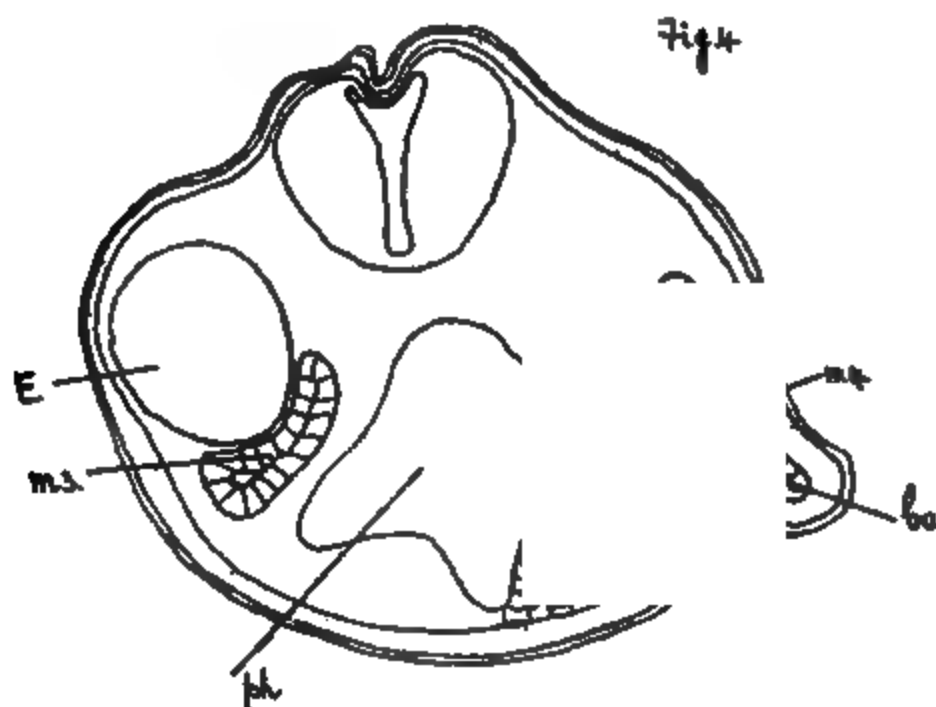
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basibranchial bar is as yet a short backward and downward projecting process of the 1st basibranchial, and to it anteriorly



is attached the united ventral ends of the 2nd, 3rd, and 4th branchial bars. By stage 9 the 2nd basibranchial is fully

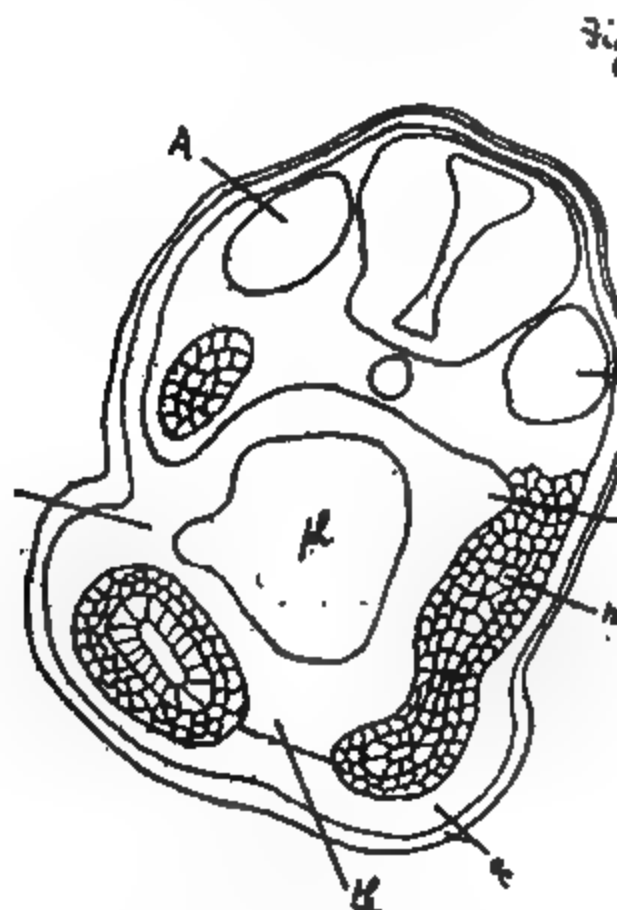


developed as a long downward and backward projecting process of the 1st basibranchial, and the basiyl has united with the

MENT OF THE HEAD MUSCLES IN

ial, the whole forming what me
plate (fig. 49).

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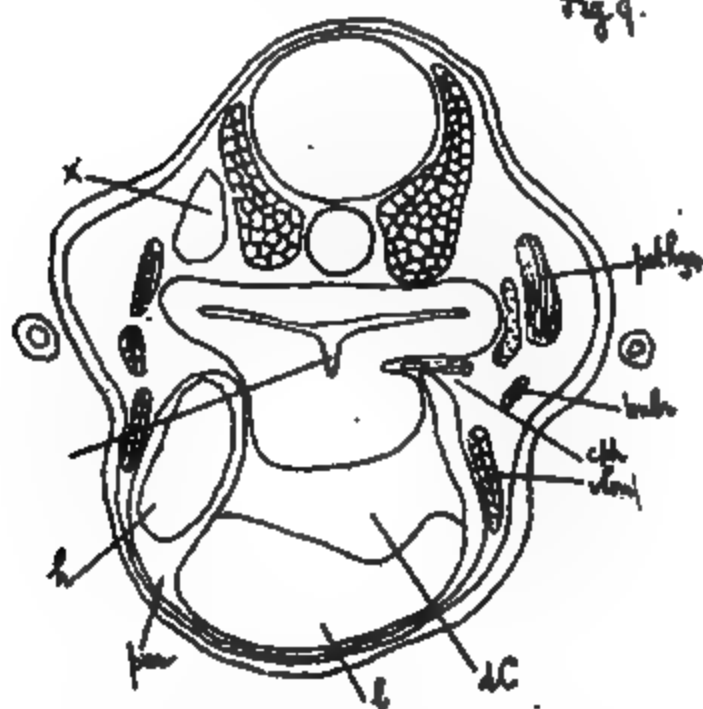
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ed, the body cavity in the lower portion has disappeared the cells have lost their epithelial form, and are muscle cells. The upper mass of cells is the

Fig 8

somatic muscle plate, the lower the splanchnic, of the segment. A few cells are seen being given myotome into the mandibular tentacle (fig. 8).

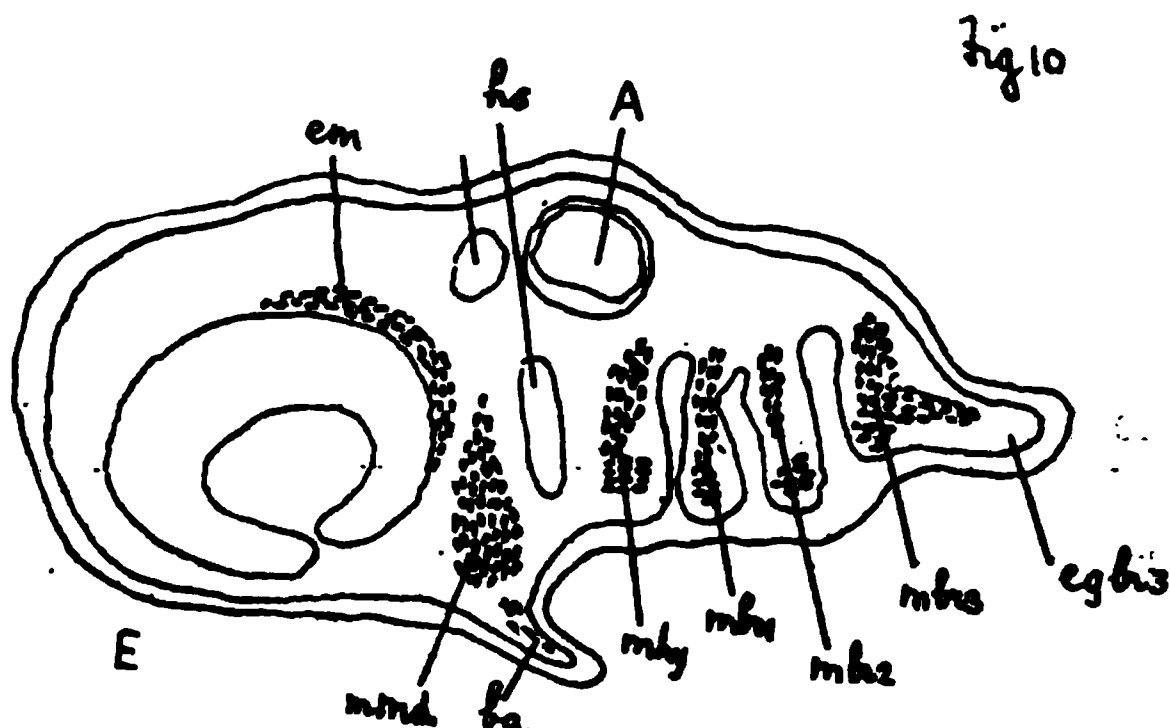
Fig 9.



7½ considerable changes have taken place in the external division (the future anterior digastric) and one (the future temporal and masseter) can be dis-

tinguished. Both are inserted below into Meckel's cartilage. The upper end of the internal division has extended upwards and takes origin from the trabecular crest, whilst the upper end of the anterior digastric lies outside the suspensorium (figs. 18, 19, 28, 41).

The masseter can shortly afterwards be distinguished from the temporal, taking origin from the anterior surface of the suspensorium, and being inserted behind the temporal into Meckel's cartilage (fig. 36). Further changes are unimportant: the upper end of the temporal extends higher up so as to take origin from the dura mater above the trabecular crest, and



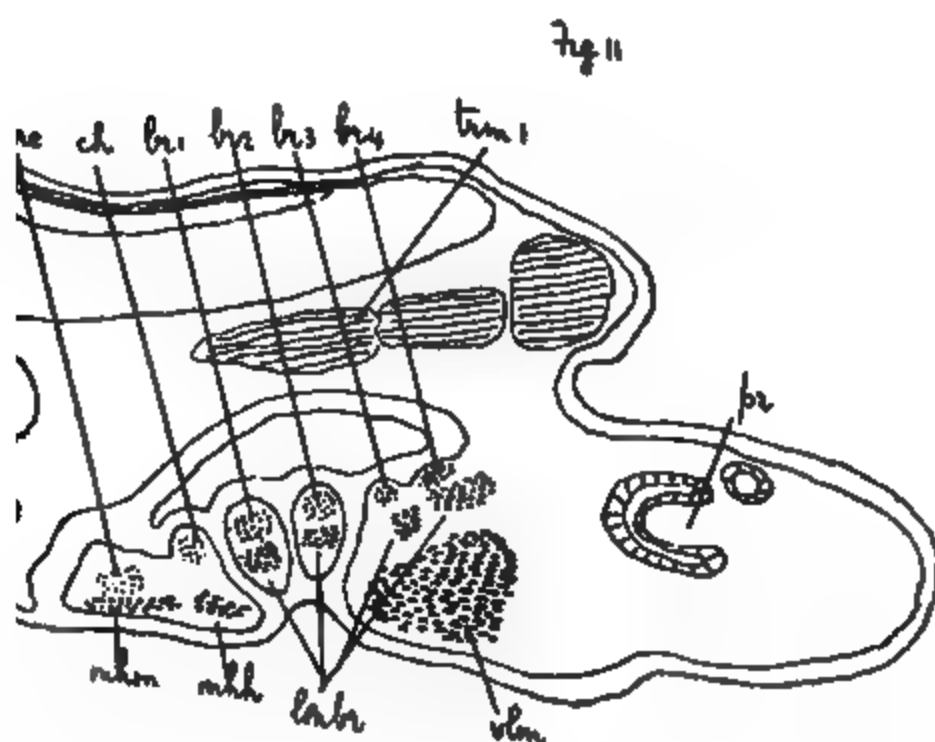
finally runs upward and backward above the auditory capsule, and overlies the anterior extremity of the muscles derived from body segments. The upper extremity of the anterior digastric similarly grows upward (fig. 39), so that it soon takes origin from the external surface of the auditory capsule.

The splanchnic muscle plates of the mandibular segment form the Meckelian mylohyoid. The two ventral ends come together, and the outer gain an attachment to Meckel's cartilages (fig. 40). The posterior edge of the meckelian mylohyoid loops back into the hyoid segment, and overlaps (ventrally) the hyoidean mylohyoid (fig. 15).

The body cavity of the hyoid segment, in stage 4, is very like that of the mandibular segment—a vertically placed cavity, lying lateral and ventro-lateral to the pharynx, lined by epithelial cells (fig. 2). By stage 5, the body cavity in the upper half has disappeared, and the muscle plate has begun to

a dorsal portion (the myotome of the hyoid) and a ventral portion (the splanchnic muscle plate) at stage 6, the upper and lower portions have separated, the body cavity in the ventral portion has appeared, and the epithelial cells have become embryonic.

The development of the myotome of the hyoid can be followed first. At stage 6, longitudinal sections (fig. 11) show that it forms a mass of cells imperfectly divided into an upper and a lower part; in the upper part,

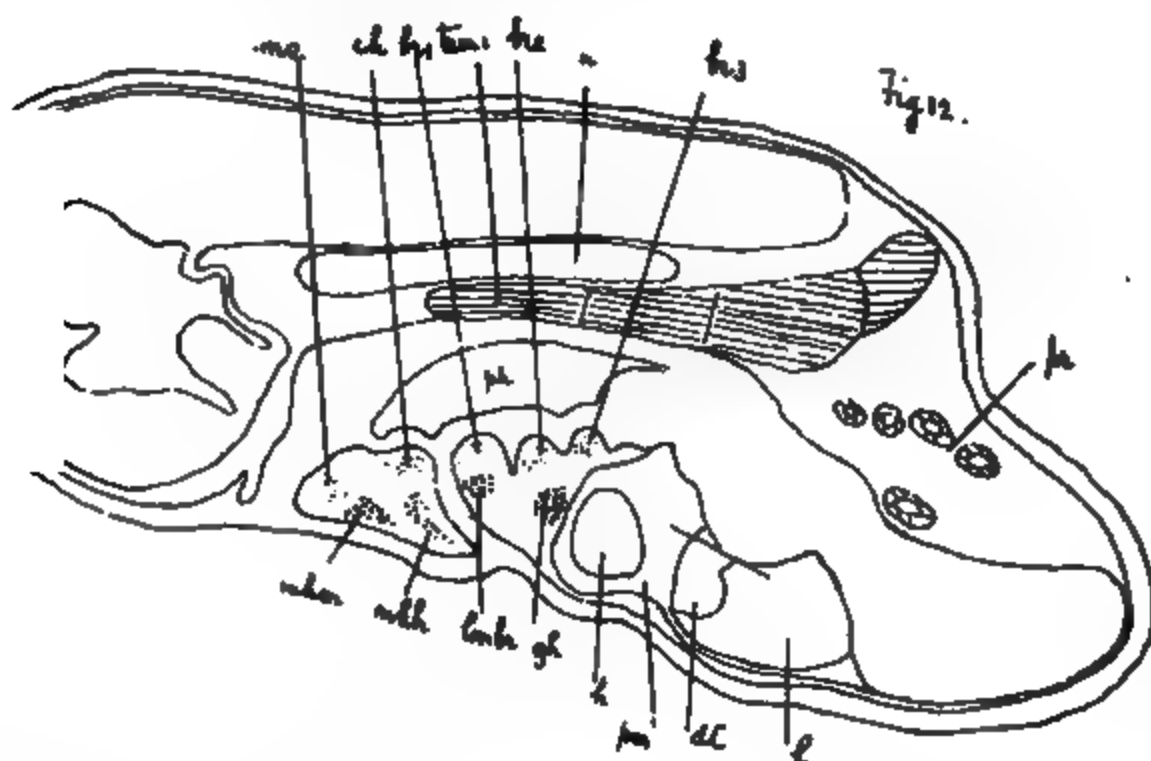


the cells are arranged with their long axes vertically, while in the lower part they are arranged horizontally. The upper part is the rudiment of the posterior digastric and external ceratohyal muscles. The lower part, which is homologous with similar masses of cells in the 2nd, 3rd and 4th branchial segments, has quite disappeared by stage 7.

It is found that the (upper portion of the) hyoid is divided into an anterior and a posterior part; the anterior is the anterior digastric, the posterior the posterior digastric, the posterior the external ceratohyal (fig. 13). The posterior digastric is a mass of long cells, the upper end of which lies outside and just behind the pharyngeal capsule, and the lower is inserted into the upper part of the external ceratohyal cartilage (fig. 18). Immediately after-

wards, however, its lower end loses its connection with the ceratohyal cartilage and grows rapidly downward and forward, and by stage 8 is inserted into the hinder end of Meckel's cartilage (figs. 24-26).

The external ceratohyal muscle, in stage 7, lies wholly in the hyoid segment. Its lower end is inserted into the ceratohyal cartilage (figs. 13, 14). By stage 9, its upper end has grown backward, and takes origin from the upper end of the 1st branchial cartilage (fig. 34). The insertion of its lower end into the ceratohyal cartilage gets further and further down,

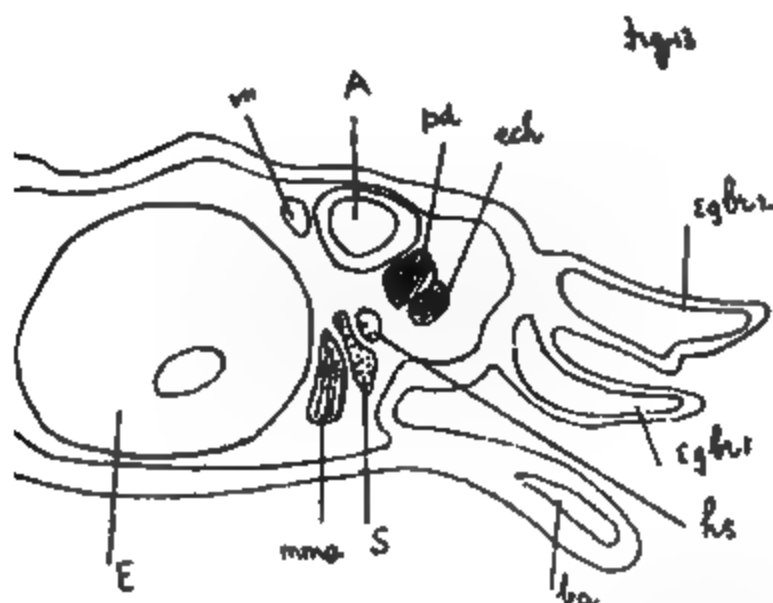


so that finally it is close to the point of union of the latter with the basibranchial plate.

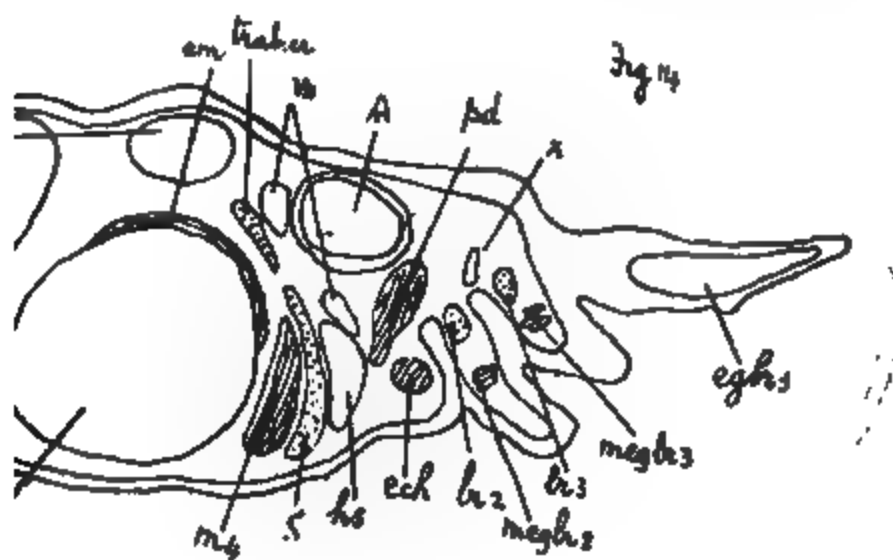
There are thus formed in the anterior part of the head three muscles—the anterior digastric, the posterior digastric, and the external ceratohyal—all directed downwards and forwards, and lying very close together, the two former inserted into Meckel's cartilage, and the last into the ceratohyal cartilage. The splanchnic muscle plates of the hyoid segment form the hyoidean mylohyoid, their inner ends unite and their outer are inserted into the ceratohyal cartilages (fig. 18). A few of the hinder fibres are inserted into the 1st branchial bars. By stage 9, it is found that the oblique direction of the gill slits has brought about the development of a median posteriorly

st from the under part of the head, and the hind myoidean mylohyoid loops into this, so that in the it is much posterior to its insertion into the (g. 35).

is formed in the four branchial segments may be



r. In stage 4, a transverse section taken through hial segment shows on each side the body cavity elial cells lying lateral and ventro-lateral to the e cavity is a mere slit in its upper part, but is



(fig. 3). Sections through the 2nd, 3rd, and 4th ments show similar appearances. Longitudinal ns show that the upper parts of the sections of the those lying lateral to the pharynx—are separated her by the branchial clefts, whereas, ventro-lateral ix, the body cavity is continuous from segment to

segment (fig. 7). This condition is brought about thus: the mesoblast sheet on either side of the pharynx splits, as described by Scott and Osborn, into two layers, an outer and an inner, lining the body cavity of the head. The developing branchial

Fig. 15

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clefts divide the upper part of this into four vertical prolongations, lined by epithelium, and communicating with the open portion of the body cavity below. By stage 5, the body cavities in the upper portions, the four branchial myotomes, have become

Fig. 16.

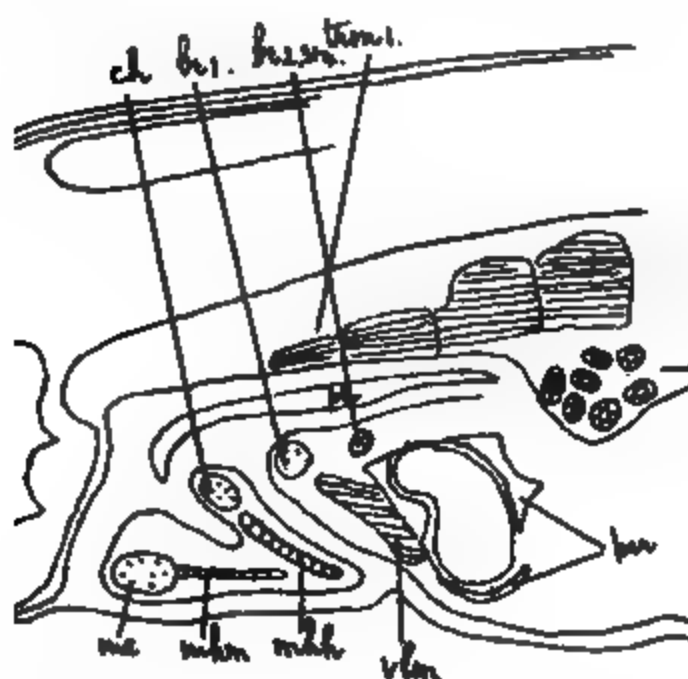
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obliterated (fig. 6); and by stage 5½, the myotomes have become separated from the epithelial cells lining the body cavity below (fig. 7). By stage 6, the cells of the myotomes have developed into embryonic muscle cells (figs. 9, 10). A change of a

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also takes place: the ventral end of stage 5 abutted on the upper end of the pleuro-lateral portion of the segment; by stage 6 it is at a lower horizontal level of the body cavity (fig. 9). This is the myotome below (and outside) the splanchnic muscle plate is not confined to the segment; it occurs also in the hyoid and mandibular segments and actually begins in the mandibular segment. The splanchnic muscles in the walls of the body cavity



the pharynx may be followed first. The two sides of the pharynx have become continuous with the pericardial cavity, which at the same time has become the pleuro-peritoneal cavity behind (fig. 9). The heart is in the pericardial cavity in stage 7; it gradually moves back as far as the 4th branchial segment (fig. 7); it gradually moves back so that the two geniohyoid muscles (in the 4th branchial segment) can come close together, the ventral longitudinal muscles can go inward towards the basibranchial

In the 4th branchial segment the constrictor pharyngis is formed immediately below the floor of the pharynx in the splanchnic mesoblast (fig. 9). The two sides unite and form a

B

fig.

sheet, which is attached on either side to the 4th branchial bar, and surrounds the developing larynx. It sends up on either

—

E

side of the pharynx, behind the 4th branchial bar, two dorsal prolongations which attach the pharynx to the trunk myotomes above (figs. 21, 37). The anterior of these dorsal prolongations

upwards, the posterior upwards and forwards, as one another. Later on, the laryngeal muscles from the fibres of the constrictor pharyngis.

Fig. 11

Fig. 12

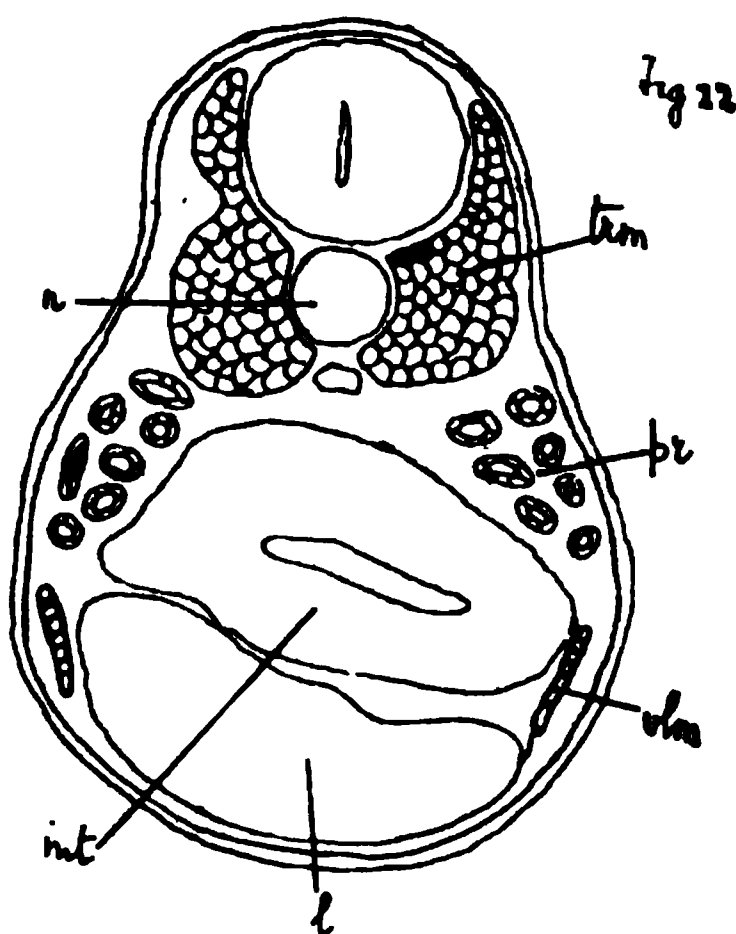
the myotomes of the 4 branchial segments are the splanchnic portions of the muscle plates,

Fig. 13

Fig. 14

ns of epithelial cells between the branchial clefts ge 6, they are vertical strips of closely aggregated cle cells, each of which is partially separated ents of the muscles it is destined to form. The

cells in the upper portions of all four myotomes are elongated vertically, in the lower portions antero-posteriorly (figs. 10, 11, 12). Four series of muscles (counting from above downwards) are formed, and each series may be taken separately. The upper ends of the myotomes—those portions, in stage 6, where the cells are elongated vertically—separate from the remainder of the myotomes by stage 7, and form the 4 petrohyoid muscles,¹ the 1st petrohyoid in the 1st branchial segment, and so on. The petrohyoid muscles become inserted into the upper ends of the four branchial arches (figs. 24–27). At first, *e.g.* in stage 8, each muscle is situated at the upper end of its own segment,

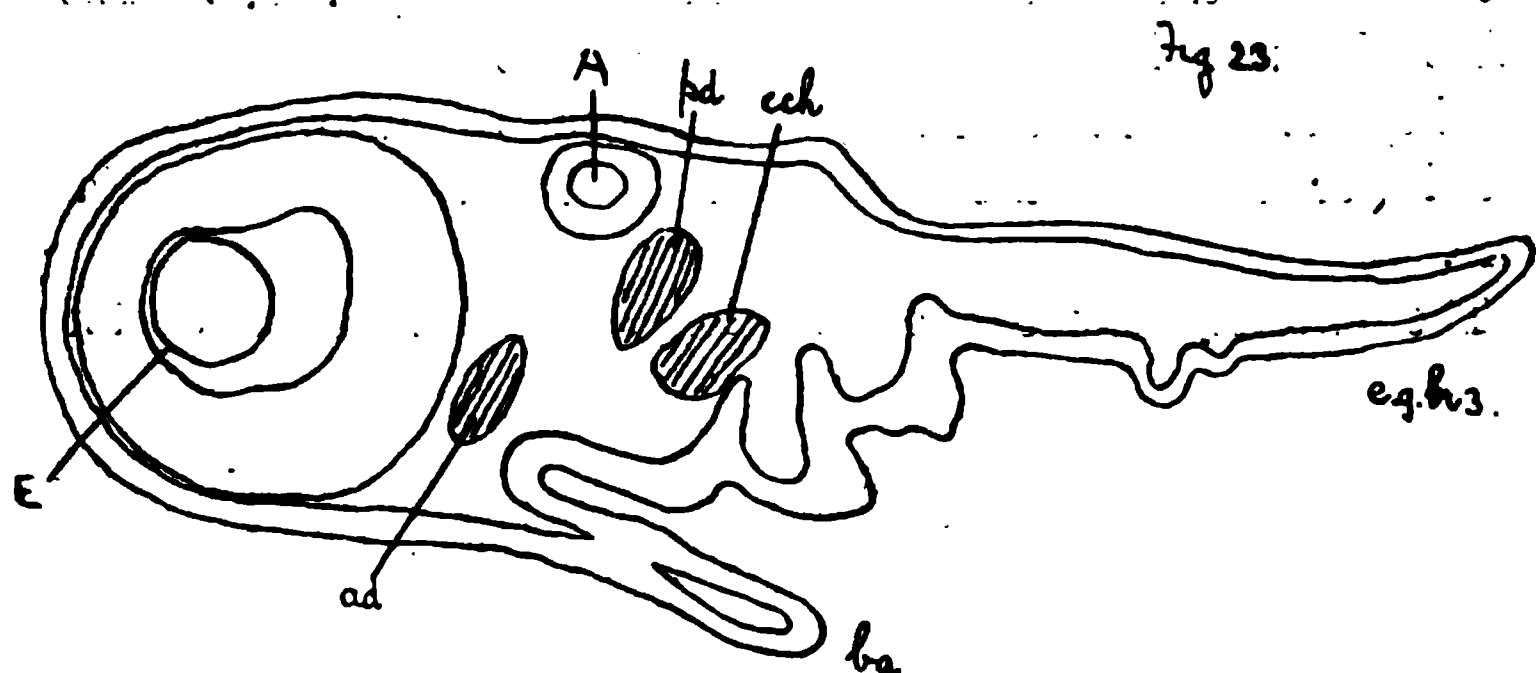


but their upper ends soon move forwards, so that by stage 11 they all arise from the posterior aspect of the auditory capsule (fig. 36). Immediately below the petrohyoid muscles are developed, the muscles of the external gills in the 1st, 2nd, and 3rd branchial segments. As stated above, external gills are developed in those segments: they are first evident, in stage 4, as short processes, which rapidly grow longer and become directed backwards, and at stage 8 gill filaments begin to develop from their under margins. Into each gill grow cells from its

¹ The four petrohyoid muscles are collectively termed by Wiedersheim (*Elements of the Comp. Anat. of Vertebrates*, tr. by Parker) the levator arcuum branchialium, but the former term is retained to facilitate comparison with the exactly similar muscles in the toad.

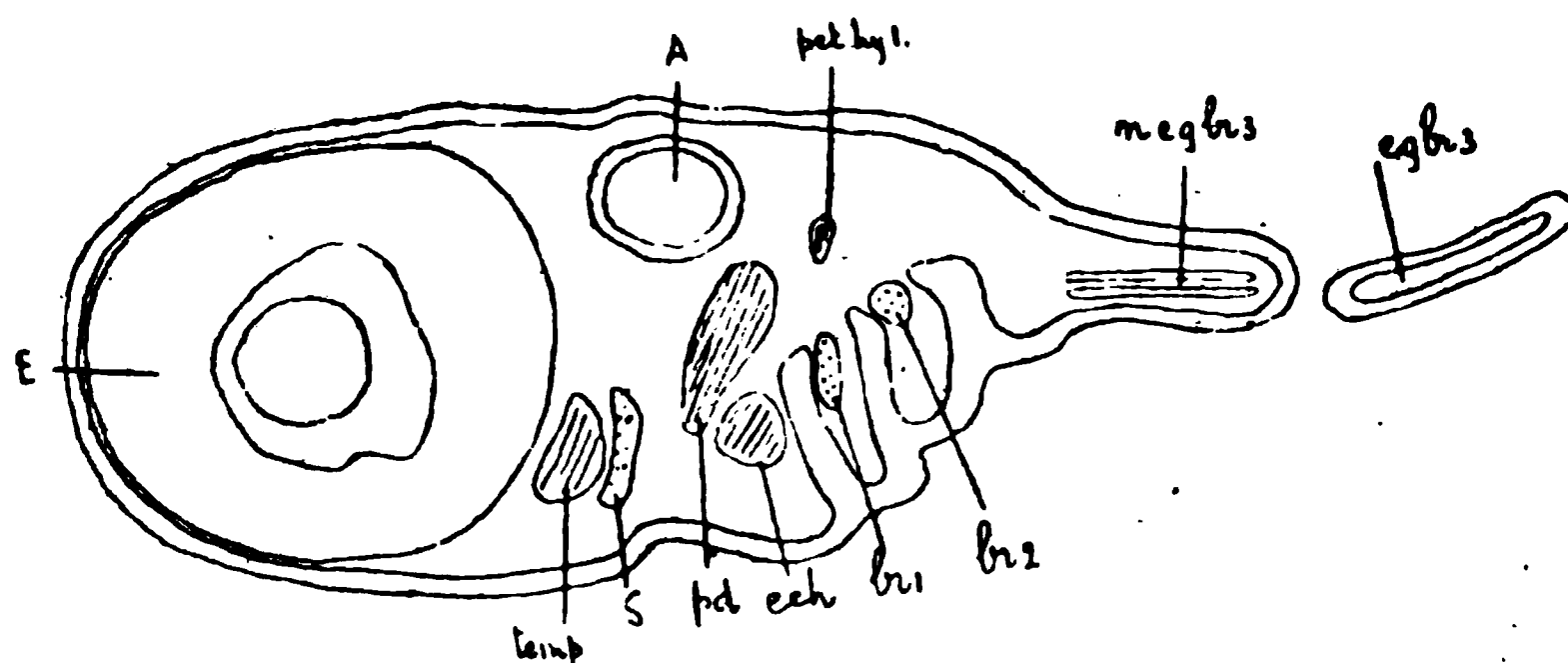
respective myotome, which develop into the long muscle fibres. At stage 6, the cells have not yet completely separated from the remainder of the myotome (fig. 10). By stage 7, they are distinct and well developed (figs. 14, 24).

Below the muscles of the gills are formed the longitudinal



muscles of the branchial bars. In stage 6, it is seen that there is a mass of embryonic muscle cells at the lower end of each branchial myotome (fig. 11). By stage 7, the three hinder masses (*i.e.*, those of the 2nd, 3rd, and 4th branchial segments)

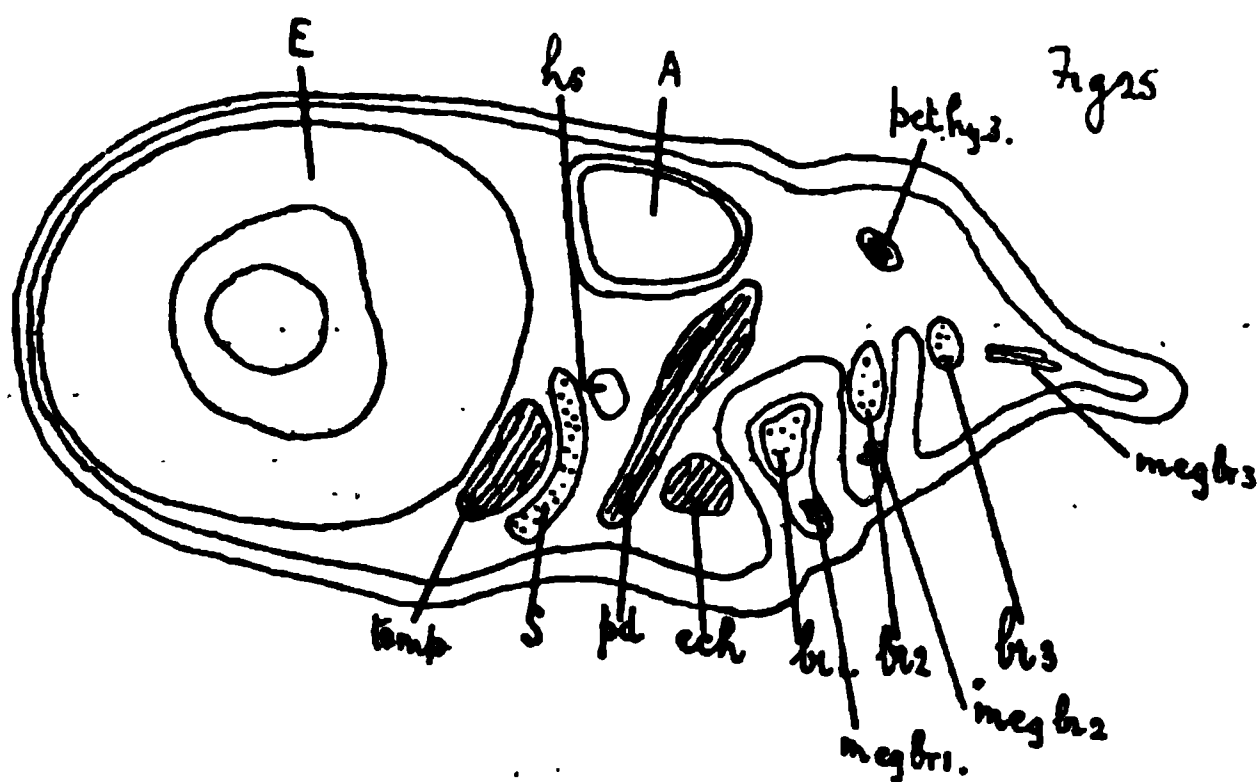
Fig 24



have united, forming a strip of longitudinally directed muscle cells, whilst the anterior one (that of the 1st branchial segment) is separate (fig. 15). The front end of the anterior one grows forward, and becomes attached by a longish flat tendon to the lower end of the ceratohyal, whilst its hind end is affixed to the

lower end of the 1st branchial. The full development of the united three hinder masses is seen by stage 11; it arises from the lower ends of the 2nd, 3rd, and 4th branchial bars, and runs forward to be inserted into the lower end of the 1st branchial bar. It also sends a slip which is inserted into the side of the 2nd basibranchial cartilage (fig. 37). The effect of these longitudinal muscles of the branchial arches, if they all acted together, would be to draw together the lower ends of the ceratohyal and all four branchial bars.

The anterior element of the longitudinal muscles of the

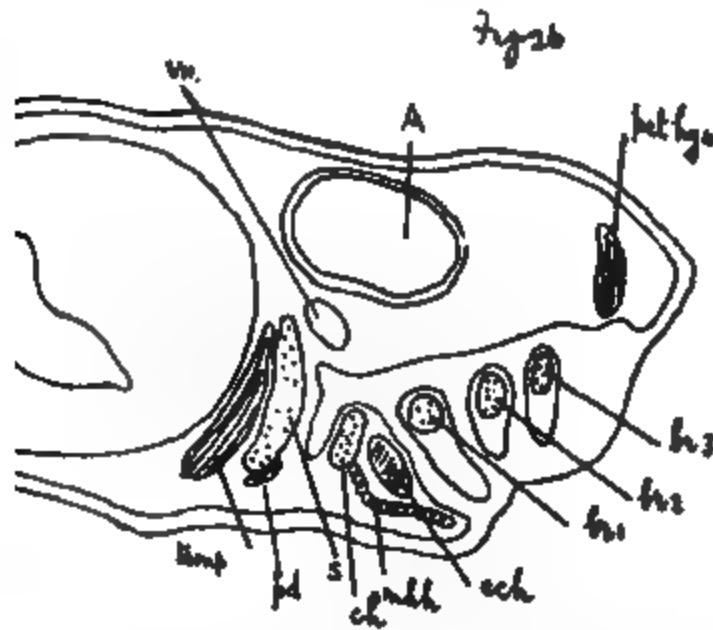


branchial arches is the most ventral muscle developed from the myotome of the 1st branchial segment. In the case, however, of the 2nd, 3rd, and 4th branchial myotomes, muscles are developed below the longitudinal muscles of the branchial arches. The ventral end of the 2nd branchial myotome forms the geniohyoid. This at stage 6 is a small mass of cells lying just in front of the pericardium, and below those cells which go to form the longitudinal muscles of the branchial arches (fig. 12). At stage 7, it still lies in the 1st branchial segment, though a little more ventrally than in stage 6 (fig. 16). In stage 8, it extends forward, lateral to the thyroid gland, but not reaching further forwards than the level of the hyoid segment (figs. 32, 33). By stage 9, it has assumed its permanent position, its front end has reached and is attached to the anterior end of Meckel's

hind end is fixed to the ventral extremity of hial cartilage (fig. 38).

Is of the myotomes of the 3rd and 4th branchial ited by stage 6, and form a flat layer of antero- ted cells, situated laterally to the pericardium, ie longitudinal muscles of the branchial arches. oes not extend further forwards than the level al bar, and its posterior edge is a little behind anchial bar (fig. 11).

anterior end of this flat strip of muscle cells is nearly as far as the level of the 1st branchial

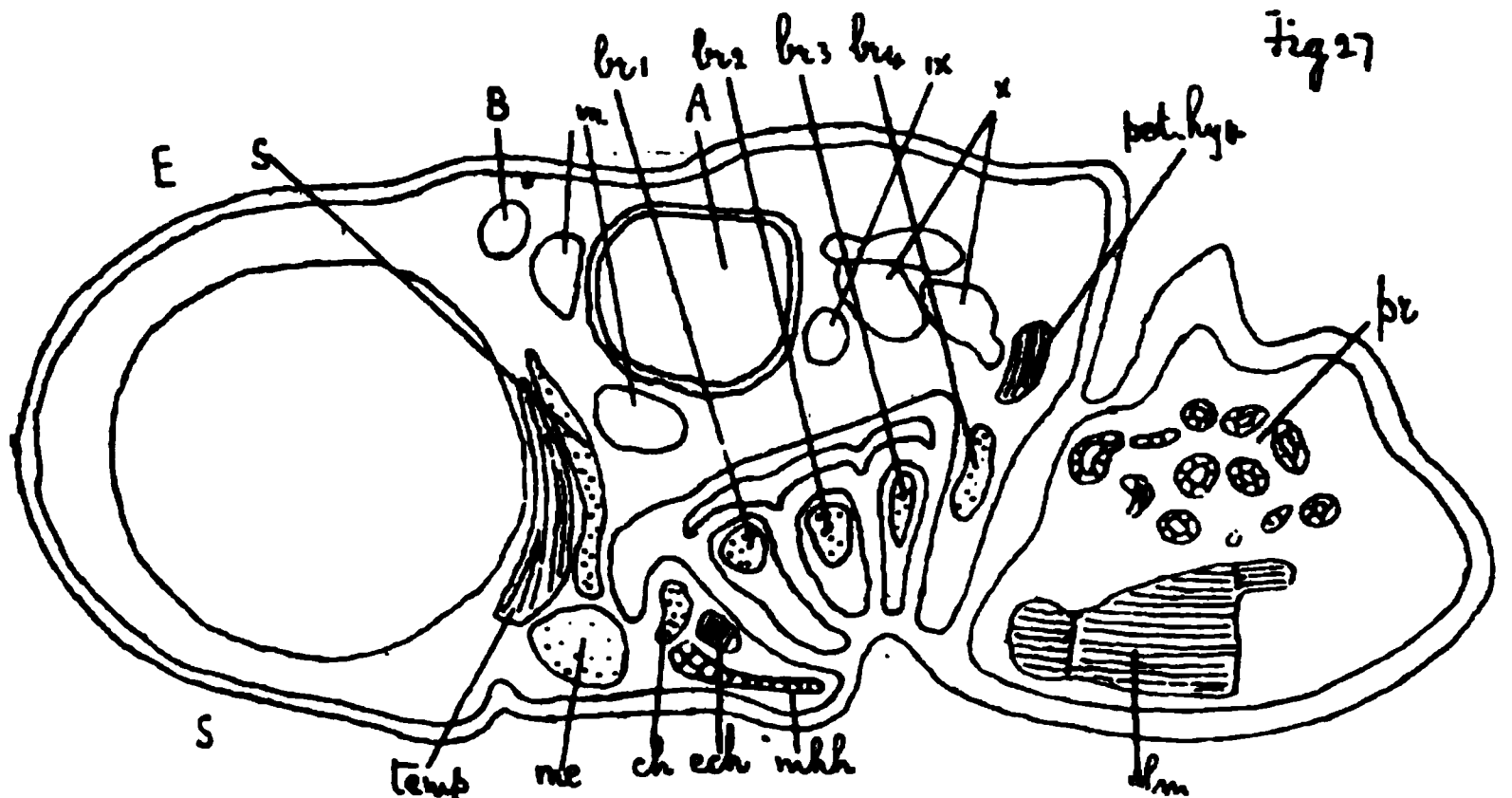


of the pericardium the strips of muscle are approximate as they are traced forward. The tended backwards, so that their posterior edge , the level of the middle of the pronephros

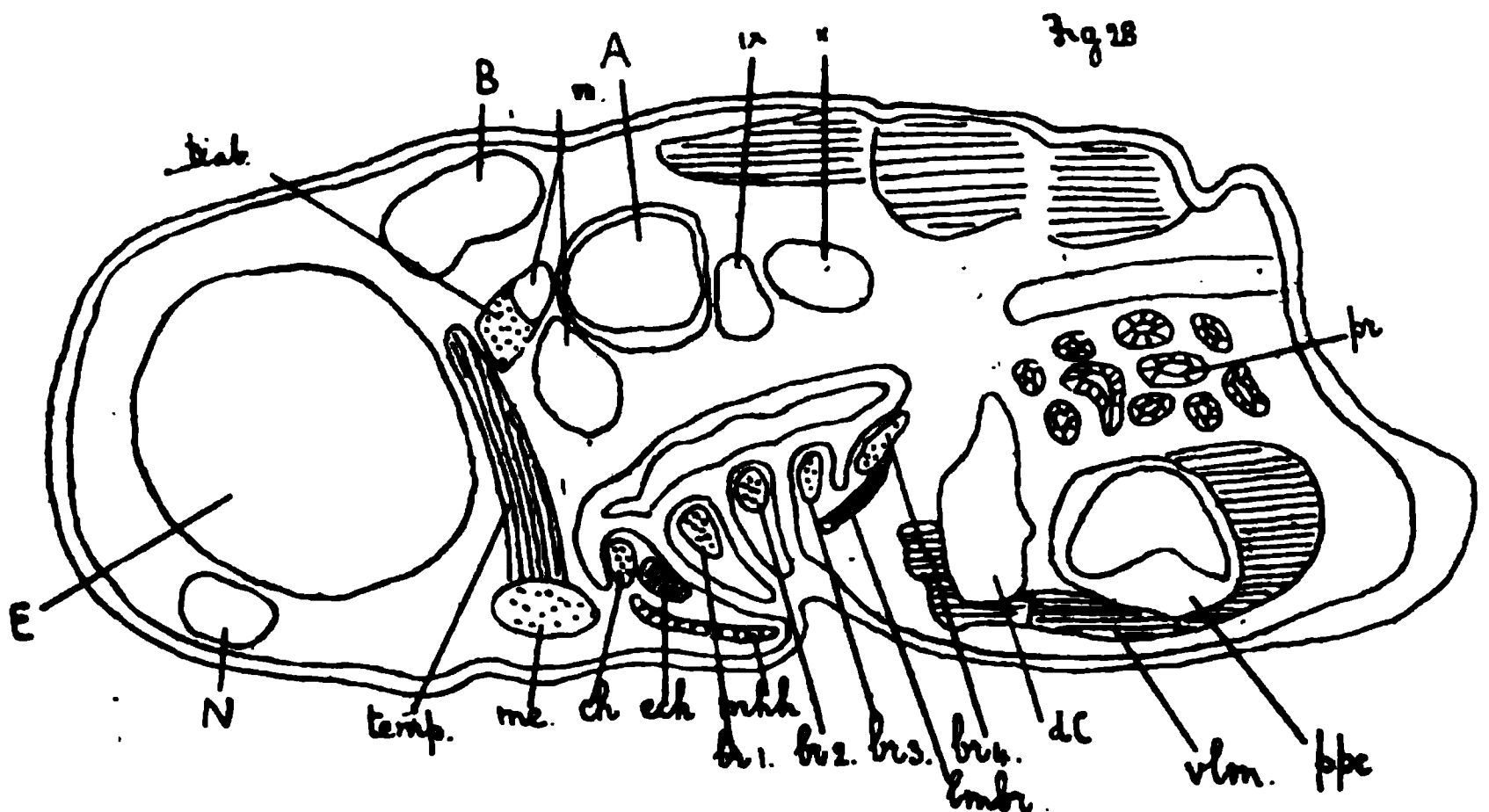
now closely approximated anterior ends of the le fibres are seen to take origin from the back ranchial and the just developing 2nd basi- this origin the muscular fibres can be traced : as the level of the 7th trunk myotome. is show that the muscles form a thin sheet on ie pericardium and pleuro-peritoneal cavity

2nd basibranchial cartilage is well formed as

a downward and backward projecting process of the 1st basi-branchial, and the anterior end of these longitudinal muscles takes origin from the whole length of its posterior surface as



well as from the back of the 1st basibranchial (fig. 38). The muscles have grown still further backwards as far as the level of the 9th trunk myotome (fig. 35). This growth backward

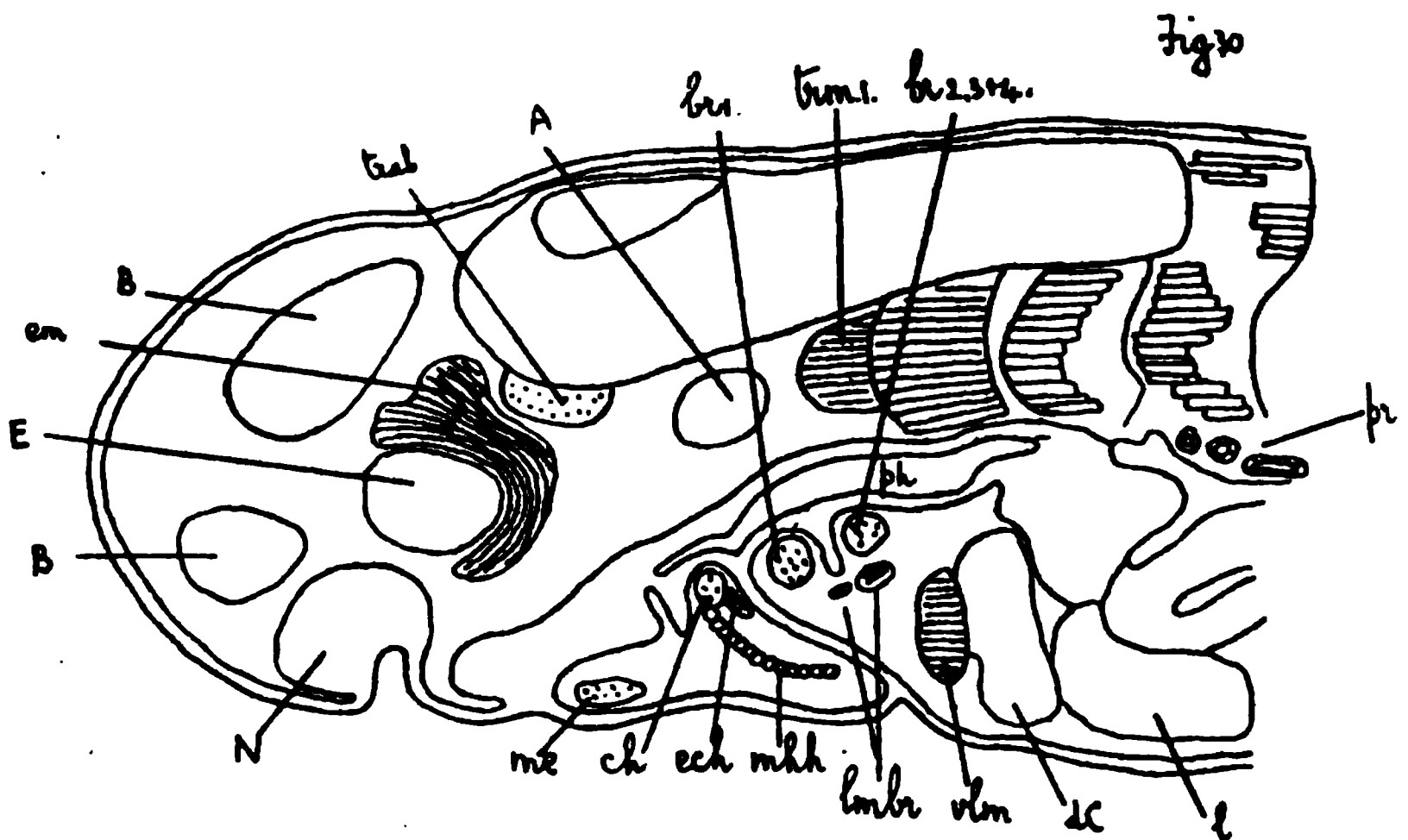


steadily continues, and by stage 13 they have reached the fore part of the tail.

Meanwhile, other changes have been taking place. The lower edges of the muscle sheets gradually spread ventrally, so that

by direct outgrowth from the 1st trunk myotome to the shoulder girdle, as in the toad. The ventral longitudinal neck muscles and the ventro-lateral trunk muscles do not take any share in forming the limb muscles.

There are three further matters to be considered—the muscular intersections in the ventral longitudinal muscles of the neck and the ventro-lateral muscles of the trunk, the splitting into layers of the latter muscles, and their relation to the shoulder and pelvic girdles. As a preliminary to the first point it is to be noted that by stage 7 the trunk myotomes have so overlapped

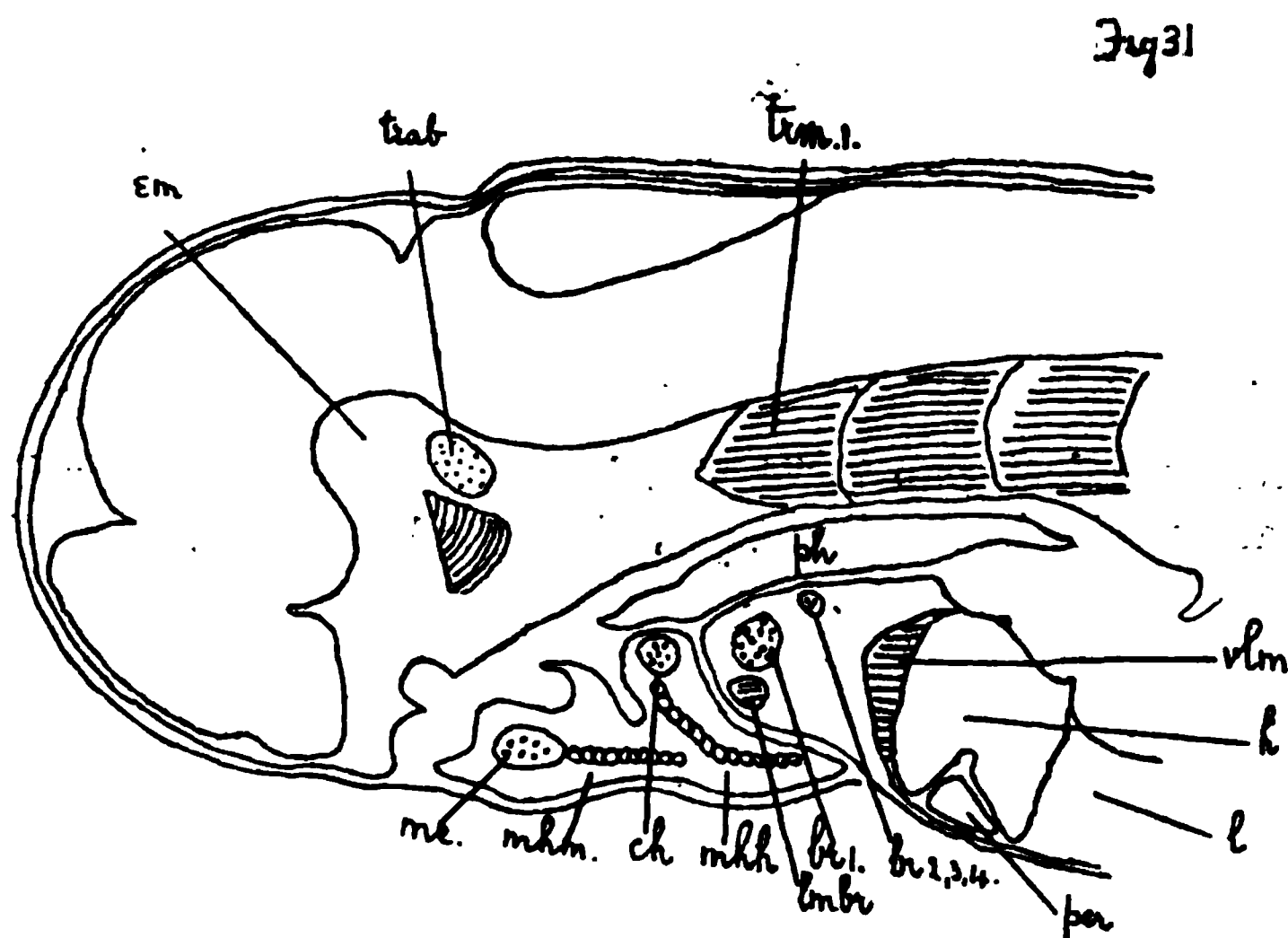


the myotomes of the head that the anterior end of the 1st trunk myotome is on a level with the 1st branchial cartilage (fig. 12); and also that, as stated above, the shoulder girdle and the pronephros are opposite the junction of the 3rd with the 4th trunk myotome (figs. 12, 29). In stage 6, no intersections are seen in the ventral longitudinal muscles; in stage 7, two are seen, one opposite the junction of the 2nd with the 3rd trunk myotome, and one opposite that of the 3rd with the 4th (figs. 15, 16). At stage 8, there are further intersections opposite the junctions of the 4th and 5th, the 5th and 6th, and the 6th with the 7th trunk myotomes (figs. 27–29).

And similarly in later stages—as the ventro-lateral muscles

grow backwards, intersections appear, each successive one being opposite one between two trunk myotomes. The myocommata into which the ventral longitudinal and ventro-lateral muscles are thus divided are of the same length as, and agree with, the trunk myotomes, the only exception being the first, which is as long as two trunk myotomes.

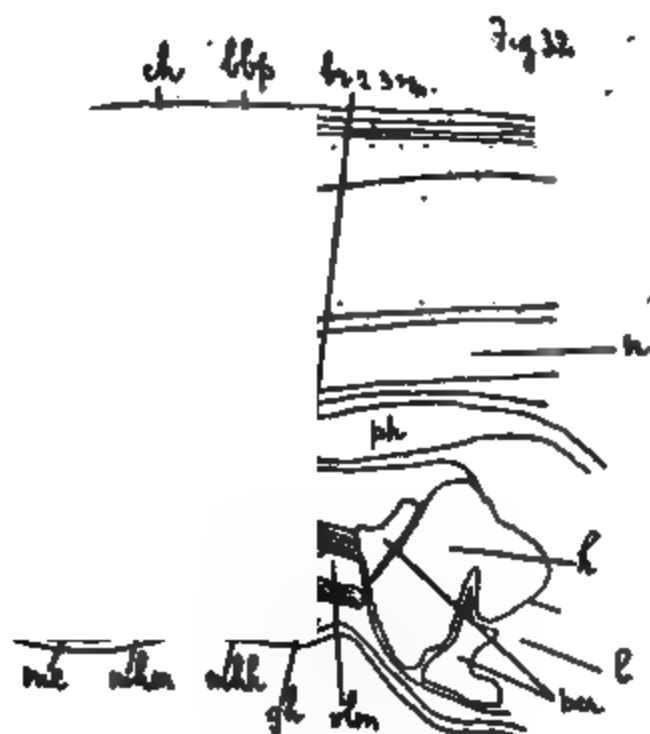
The segmentation of the trunk, as expressed in its myotomes, seems to determine, if not the actual occurrence of segmentation, at all events its sites in the ventral longitudinal neck and the



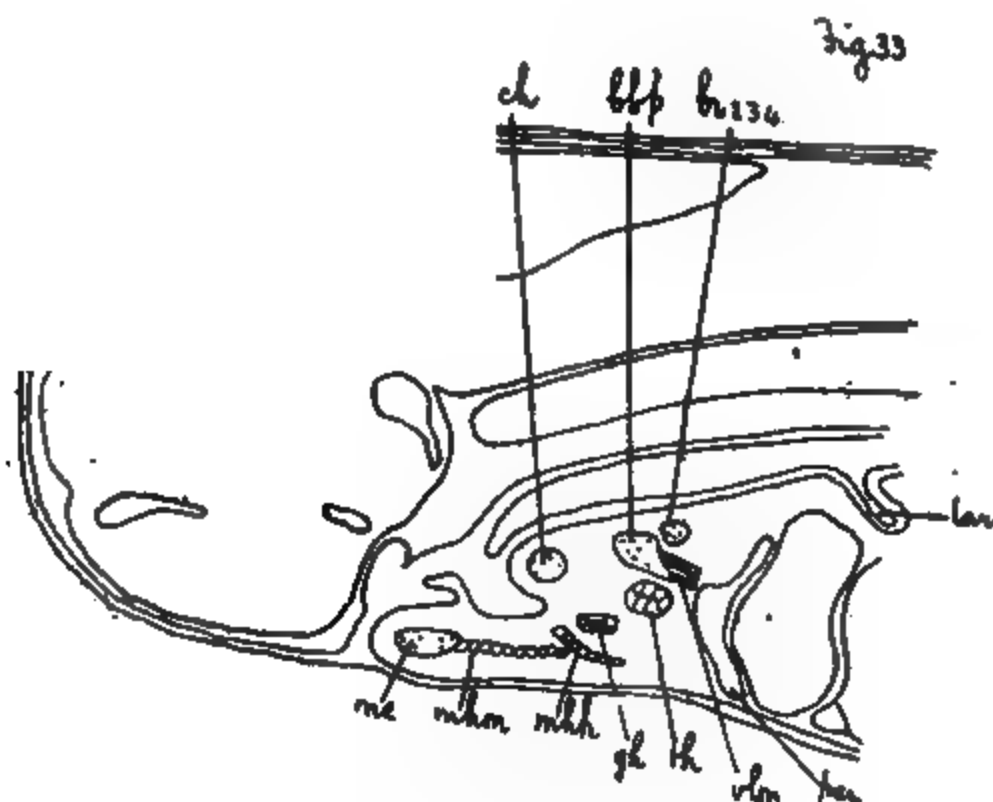
ventro-lateral trunk muscles, which are formed later in development by backward growth from certain head segments.

Up to stage 8, the direction of the muscular fibres of the ventral longitudinal and ventro-lateral muscles is antero-posterior (fig. 29). At stage 9, whilst that of the former is still antero-posterior, behind the level of the (future) shoulder girdle their direction is backward and slightly upward, though those nearest the ventral edge of the muscle remain antero-posterior (fig. 35). There is up to this stage one muscular sheet only. This condition persists in the ventral longitudinal muscles of the neck. In later stages the ventro-lateral muscles of the trunk become split up into four layers—the two external

obliques, the internal oblique, and the transversalis. There is no distinct rectus abdominis developed in the stages of growth



investigated (i.e., up to 24 mm. long), though in the sexually mature animal, according to Wiedersheim,¹ a distinct rectus is



present. In the ventral part of the ventro-lateral muscles, however, the muscular fibres which have a persistent antero-

¹ *Lcc. cit.*

re much smaller than those of the remainder

e is developed by stage 11, but up to stage
of the ventro-lateral muscles are inserted

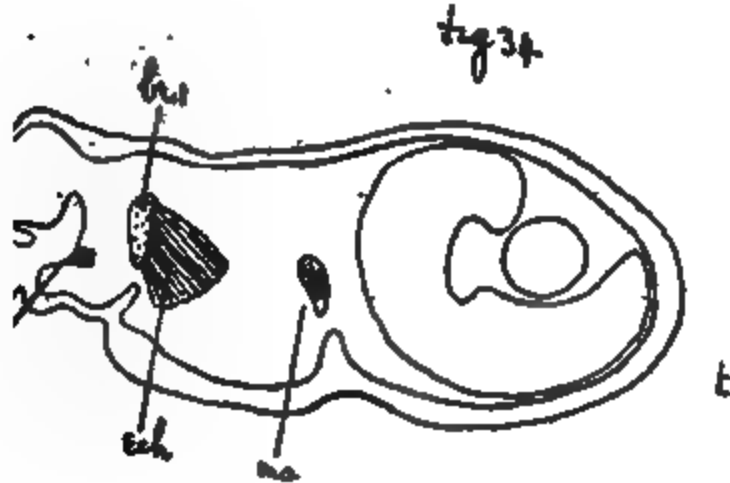


Fig 20, however, a median rhomboid-shaped
n is developed between the ventral ends of
its of the shoulder girdle, and the most



-lateral muscular fibres are inserted into its
5).

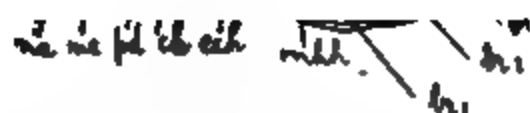
s developed by stage 18, and some of the
tro-lateral muscular fibres become inserted
ority pass, internal to it, into the ventro-
he tail.

The ribs developed in the septa betw the trunk, do not extend into those betwe ventro-lateral muscles.

Tongue muscles.—There is no trace of a by which time the thyroid has separ epithelium. A little subsequently, a formed in the floor of the mouth, betw and anterior to the site of the thyroid. There is also developed a forward proj membrane in front of the anterior end of and the lower ends of the ceratohyal cart

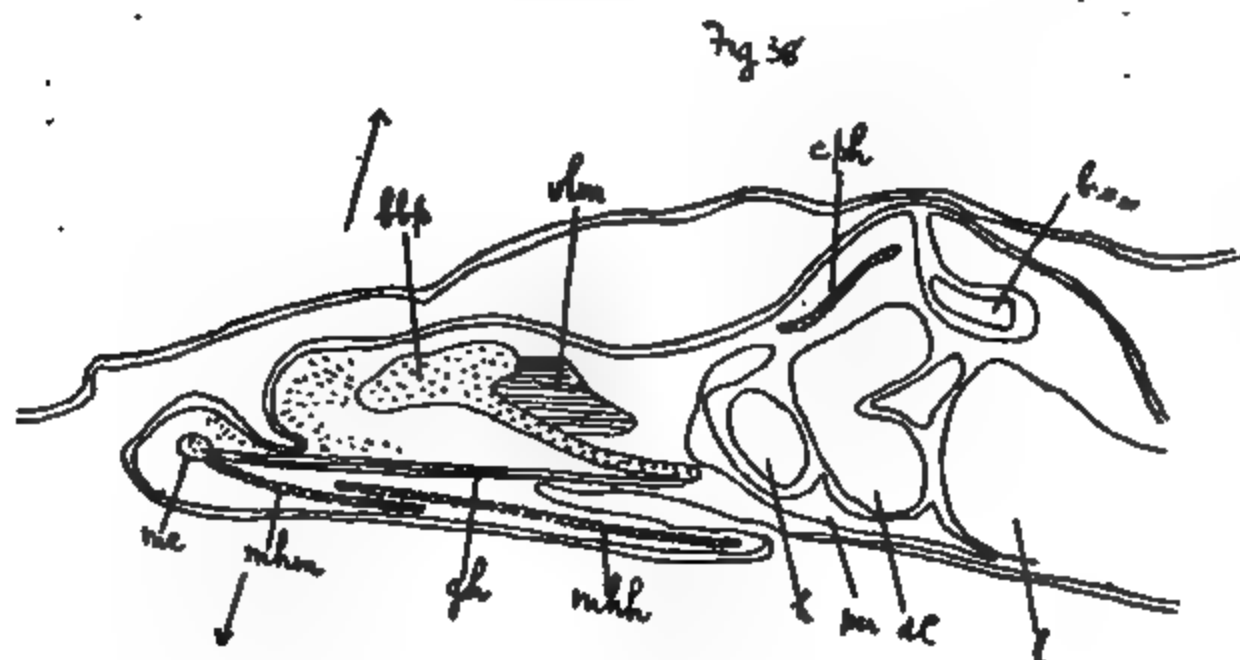
Emb

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and the forward projecting fold are covered by a stratified epithelium, whilst the intervening space is covered by a thin single-layered one. No muscles are developed until much later, at a time when the fore and hind limbs are well developed; then the scattered mesoblast cells lying below the depression increase in numbers, and form on each side a genioglossus muscle, which becomes attached to the anterior end of Meckel's cartilage (figs. 44, 46). These cells probably have their origin in those which are seen being given off from the maxillary splanchnic muscle plates in stage 6, but their genesis cannot be traced with certainty. They are certainly found lying just below the buccal epithelium before the geniohyoid muscle grows forward, as described above, from the ventral end of the myotome of the 2nd branchial segment. No hyoglossus muscle

the stripes are formed by the aggregation of cells from an undifferentiated or uniform sheet of mesoblast, and each divides into a dorsal—somatic—and a ventral—splanchnic—portion, in



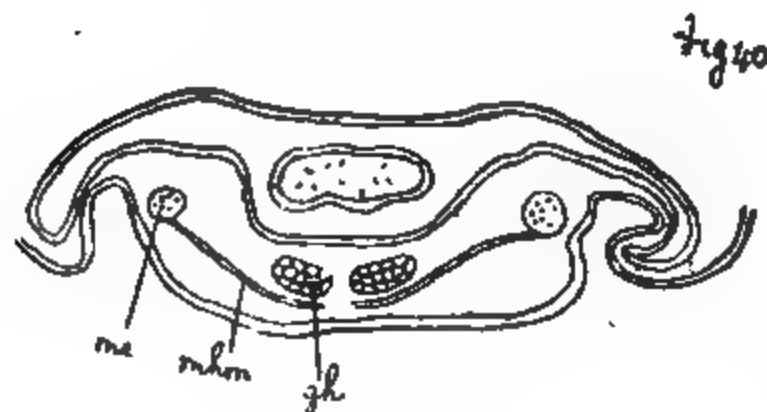
the newt they are formed by the conversion of the epithelial cells lining the upper and lower portions of the head cavities into muscle cells.

The muscle plates being formed in this diverse fashion in the

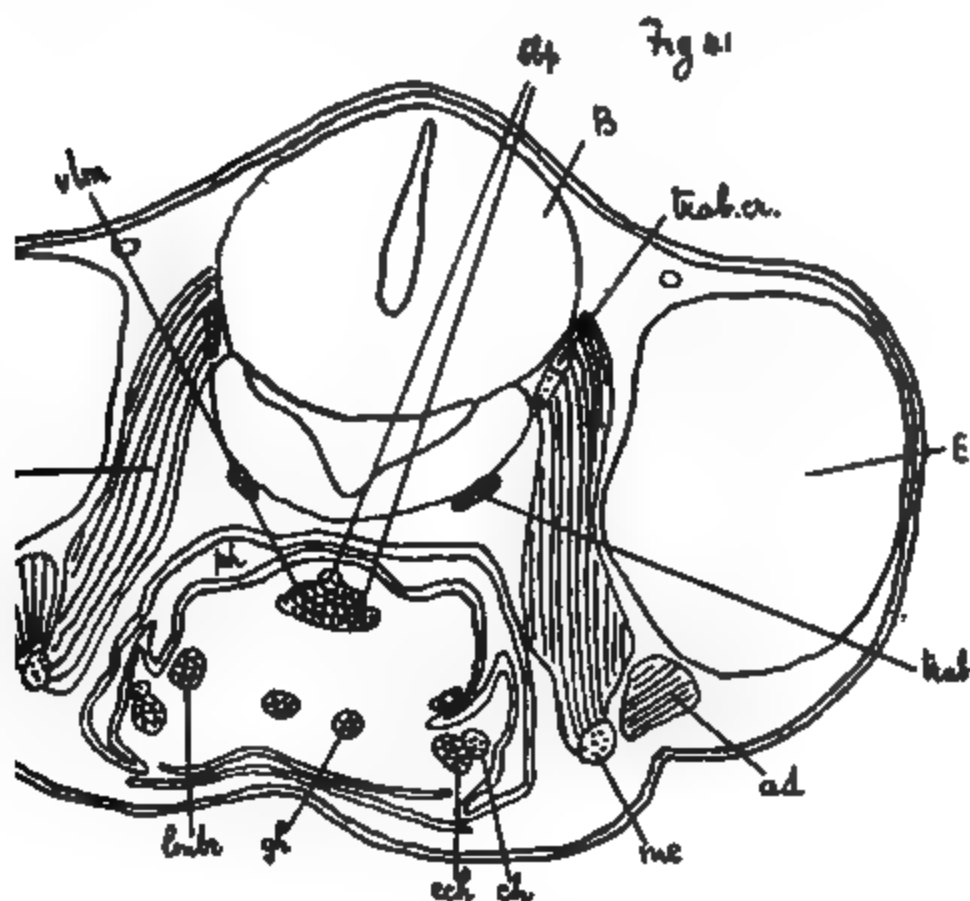
two animals, their development into muscles runs along closely parallel lines.

The splanchnic muscles may be taken first. The differences

Following: In the toad, the meckelian and hyoidean form one continuous sheet, whereas in the newt they are separate. In the newt there is no submentalis. In both



heart is developed in the 1st, 2nd, and 3rd branchial arches. The pharyngeal and laryngeal muscles, developed in the 4th and 5th branchial segments, are slightly different in the two



In the toad, during the tadpole stage, there is no pharyngeal constrictor, and only the rudiments of the laryngeal constrictor are attached on either side to the 4th branchial arch. At metamorphosis, a pharyngeal constrictor is

developed, though feebly, with one prolongation upward on either side, which is attached to the outer side of the trunk myotomes. In the newt, the pharyngeal muscles are developed early as a well marked sheet of muscle underlying the pharynx, surrounding the rudimentary larynx, attached laterally to the 4th branchial cartilage, and sending up, behind the 4th branchial cartilage on each side, two dorsal prolongations, to attach the pharynx to the outer side of the trunk myotomes.

In the toad, a tongue (which corresponds to the tuberculum impar of mammals) is developed shortly before metamorphosis,

7

and from it grow well marked genioglossus and geniohyoid muscles; whereas in the newt there is no protuberance in front of the site of the thyroid downgrowth, but merely a depressed area, beneath which a feebly marked genioglossus muscle is developed, relatively late, and there is no hyoglossus muscle. There is also in the newt, but not in the toad, a forward projecting fold of mucous membrane in front of the basibranchial plate.

As regards somatic muscles, the first important difference to be noted is that, in the toad, in correspondence with the development of a suctorial mouth, and the correlated disposition of

scles, the myotome of the mandibular segment
 erse axis, so that it lies across, and on the
 of the hyoid segment; and it is not

of the head segment is the
 Meckel's cartilage and hyoid
 segment in the newt larva
 Meckel's cartilage is both
 short, with no suctorial
 type

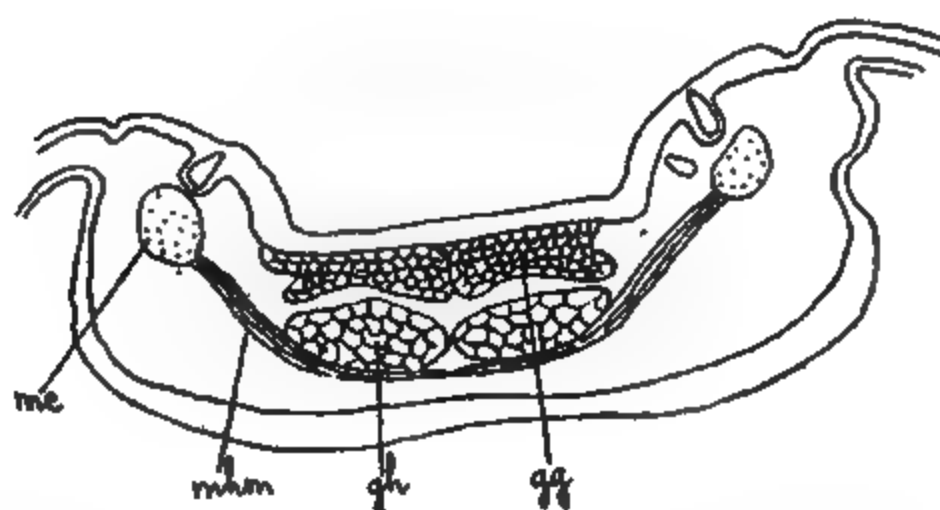
low

slan

u

until metamorphosis that, with the loss of a suctorial mouth
 elongation of Meckel's cartilage, and backward rotation of the
 ventral end of the suspensorium, that the mandibular muscles

Fig 44



lie again in a more or less dorso-ventral position. On the other
 hand, in the newt no suctorial mouth is formed, and the man-
 dibular myotome preserves its original dorso-ventral position.
 The muscles eventually formed from the mandibular myotome

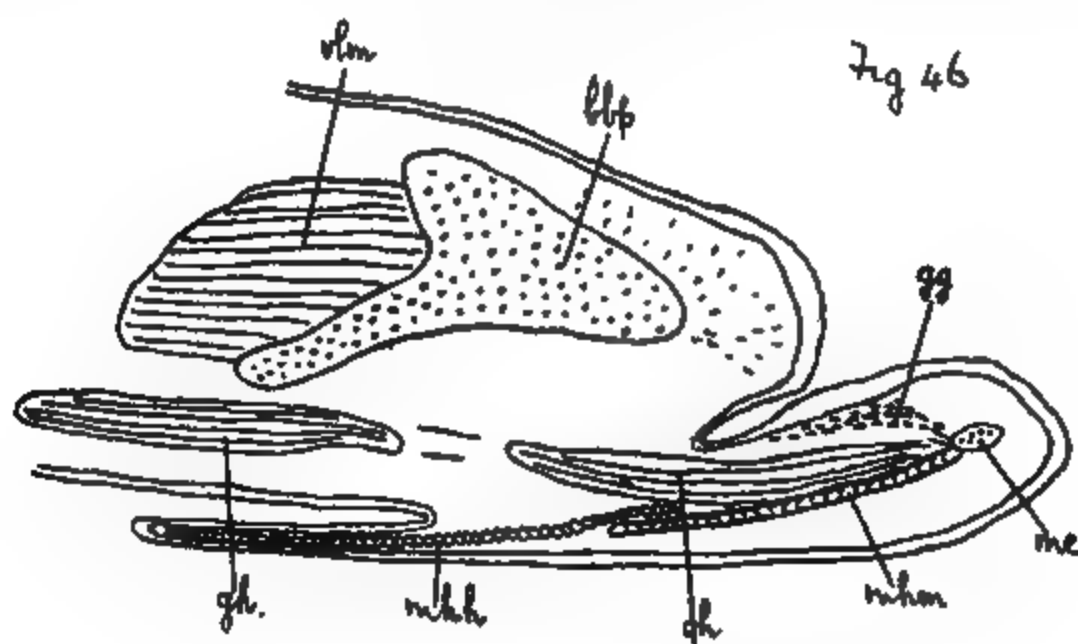
are very similar in the two animals—a temporal, masseter, and anterior digastric are differentiated in both; though in the newt, unlike the toad, no pterygoid is separated off from the temporal as a distinct muscle.

The somatic muscles of the hyoid segment present interesting

Fig 45

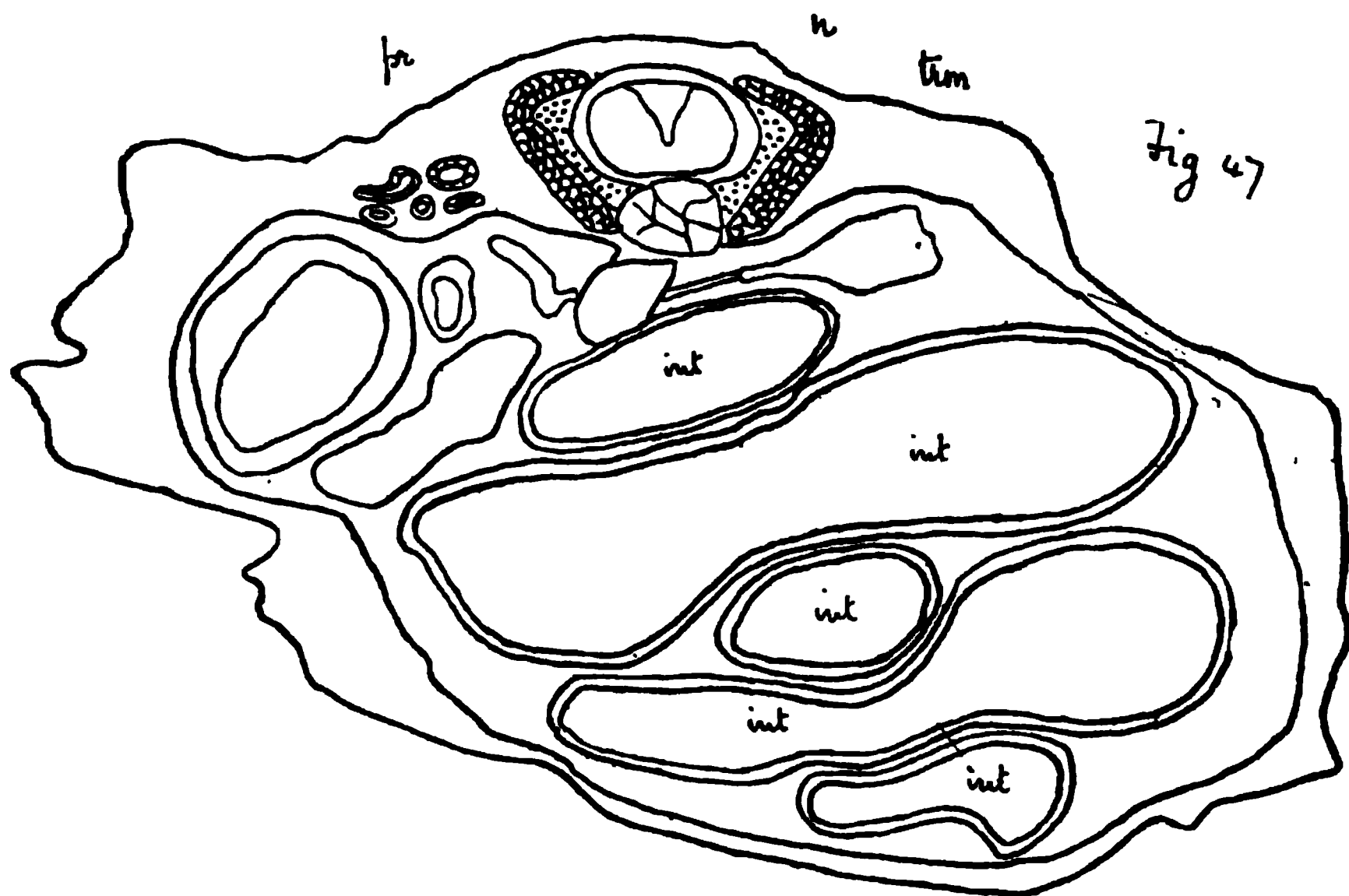
Fig 46

differences. In the tadpole of the toad, the myotome separates into a dorsal portion, the posterior digastric, which passes from the orbital plate of the suspensorium to the top of the ceratohyal cartilage, and a ventral longitudinally directed muscle,



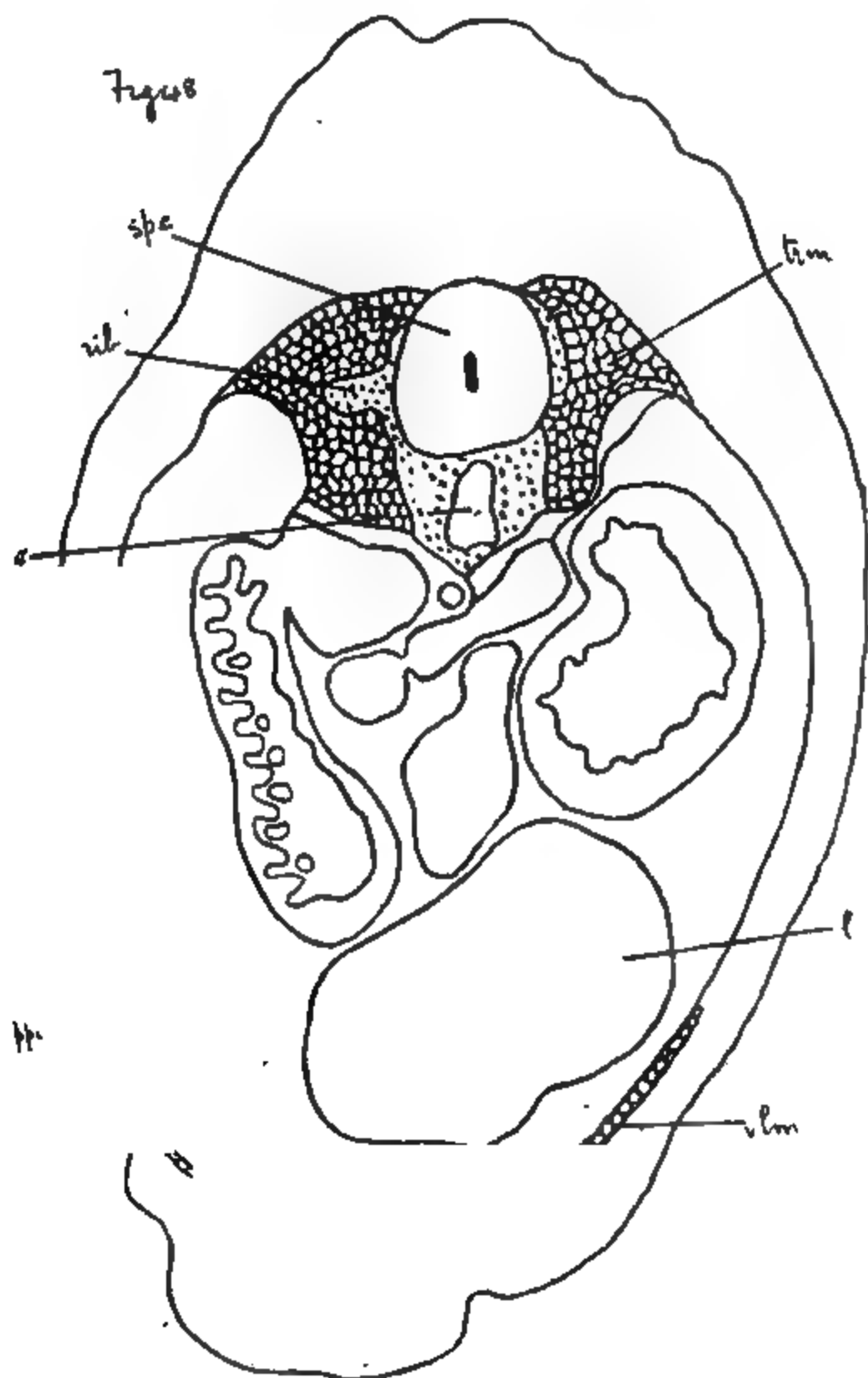
which passes from the ceratohyal to Meckel's cartilage; at metamorphosis, the ventral muscle disappears, and the ventral end of the posterior digastric shifts from the upper end of the ceratohyal to the posterior end of Meckel's cartilage. In the newt, no ventral portion is formed (though there is possibly a

rudiment of it during stage 6), and the myotome develops into the external ceratohyal and posterior digastric muscles. The latter at first is inserted into the top of the ceratohyal, but very early—before, in fact, the cells become striped muscle cells—shifts to the hind end of Meckel's cartilage. The original function of the muscle—that of an elevator of the ceratohyal—is thus early lost in the newt, whilst it is preserved during the tadpole life of the toad. There is no representative in the toad of the external ceratohyal muscle.



The somatic muscles of the four branchial segments may be taken together. The gill muscles, so well developed in the newt, are absent in the toad. Otherwise the resemblances are close. A petrohyoid muscle is developed from the upper end of each myotome in both animals. In the newt, from the middle portions of the last three branchial myotomes and the lower portions of the 1st branchial myotome, is formed a well developed series of longitudinal muscles, connecting together the ventral ends of the four branchial and the hyoid arches. In the tadpole, the only representatives of these muscles are the muscle which, developed from the 2nd

branchial myotome, passes from the ventral end of the 2nd branchial cartilage to the ceratohyal, and the muscle which, developed in the hyoid segment, passes from the ceratohyal



to Meckel's cartilage. This last muscle has no representative in the newt, though, as stated above, there is for a time a possible representative of it developed at the ventral end of

myotome. The feeble development, and disappearance at metamorphosis, of these longitudinal muscles in the toad may be correlated with the shortness of its aquatic tadpole stage.

In newt and toad, the geniohyoid is developed from the myotome of the 2nd branchial myotome.

In newt, the ventral longitudinal muscles of the neck and lateral muscles of the trunk are developed from the myotomes of the 3rd and 4th branchial myotomes. In the toad¹ the ventral ends of the 3rd and 4th branchial myotomes forming during tadpole life a feebly developed muscle, extending backward ventro-lateral to the

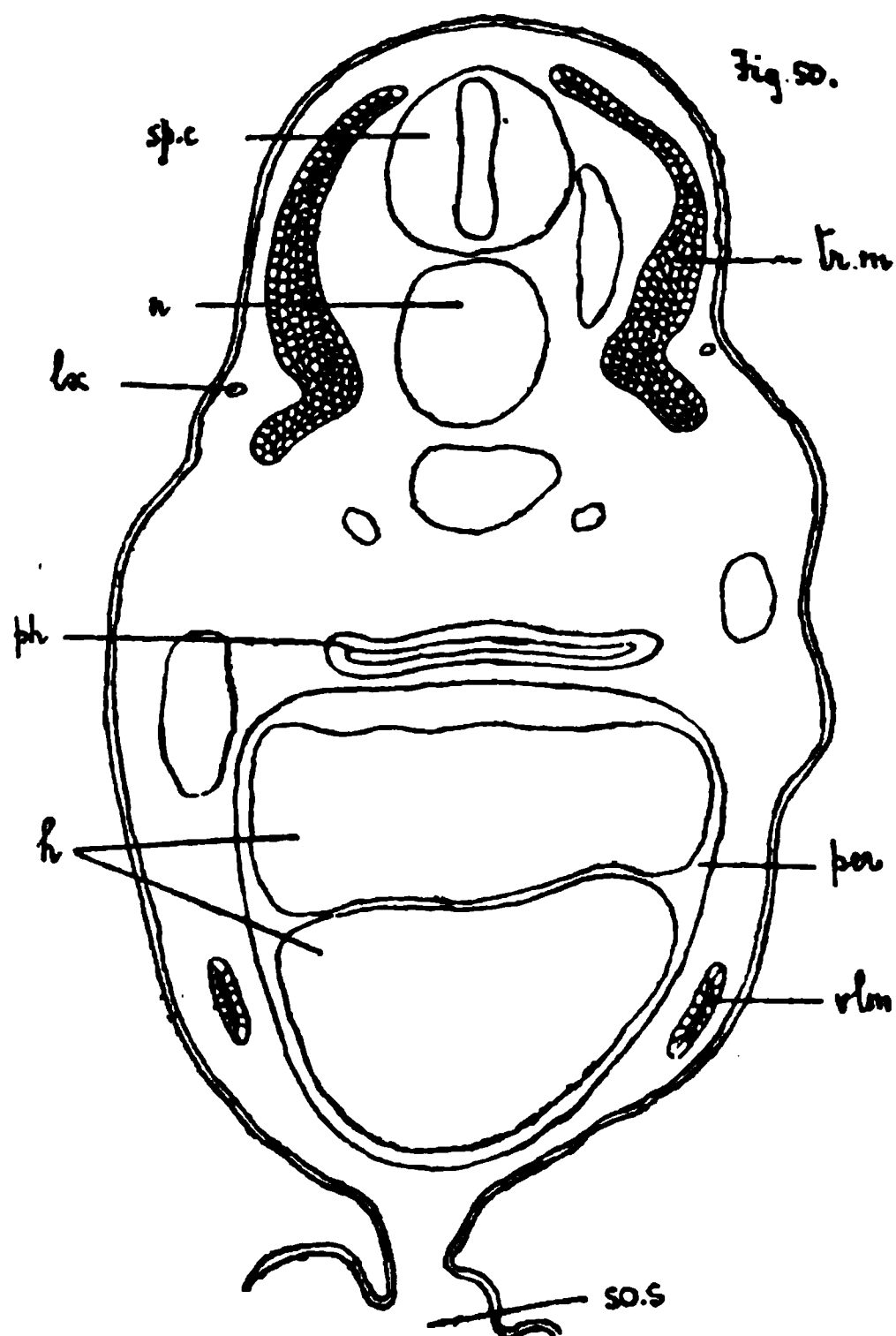
μ

FIG. 49.

muscle, and as only developing and extending back to the shoulder girdle at metamorphosis, to form the ventral longitudinal muscles of the neck. The above described results suggest that in the toad, at metamorphosis, these muscles extend beyond the shoulder girdle, and formed the lateral muscles of the trunk. This I find to be the case: from the sections, which I had fortunately kept, it is seen that whereas during tadpole life the abdominal wall muscles, the only ones present in the trunk being the lateral ones derived from the trunk myotomes, at metamorphosis the longitudinal muscles of the neck extend not merely as far as the shoulder girdle, but beyond, and form the feebly developed ventro-lateral muscles of the trunk (Fig. 48).

¹ *Loc. cit.*

Thus the only differences between the two animals are, that whereas in the newt extension backwards takes place steadily from the first, and the ventro-lateral muscles of the trunk are highly developed, in the toad there is a pause in backward growth during tadpole life, extension to and beyond the shoulder girdle occurs at metamorphosis only, and the ventro-lateral trunk muscles are feebly developed.



In these Amphibia, then, the ventral longitudinal muscles of the head¹ and neck and the ventro-lateral muscles of the trunk are developed from the ventral ends of the myotomes of the second, third, and fourth branchial segments; and the dorso-lateral and limb muscles are the only somatic muscles formed from the body myotomes.

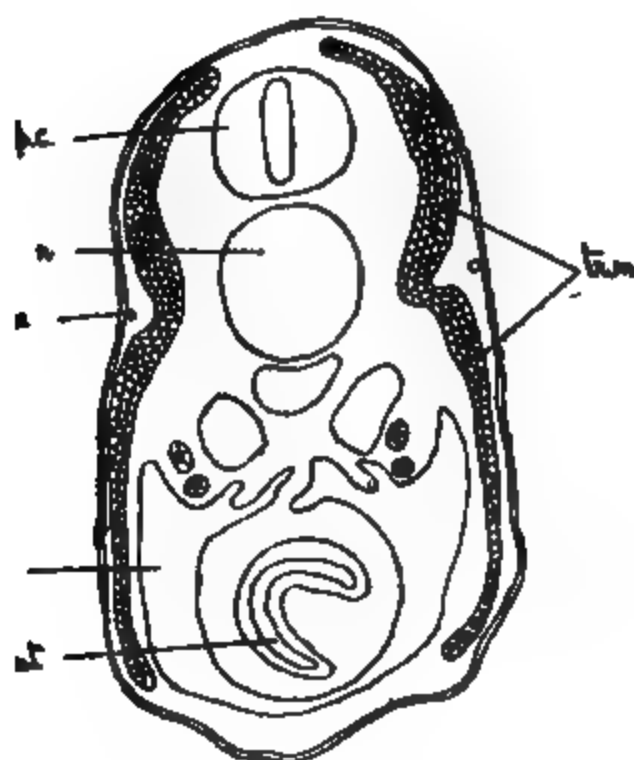
Ventro-lateral body muscles derived from head segments are

¹ Counting the geniohyoid as the ventral longitudinal muscle of the 'head.'

acraniate Vertebrata, and must therefore have
ready segmented Vertebrate. It is in accord
a partition into myocommata, corresponding
myotomes, occurs *pari passu* with their growth
the body.

show an interesting stage intermediate be-
tween acraniate Vertebrata and Amphibia, in that
muscles are formed from head segments, but only
as far as the shoulder girdle. A transverse

fig. 51

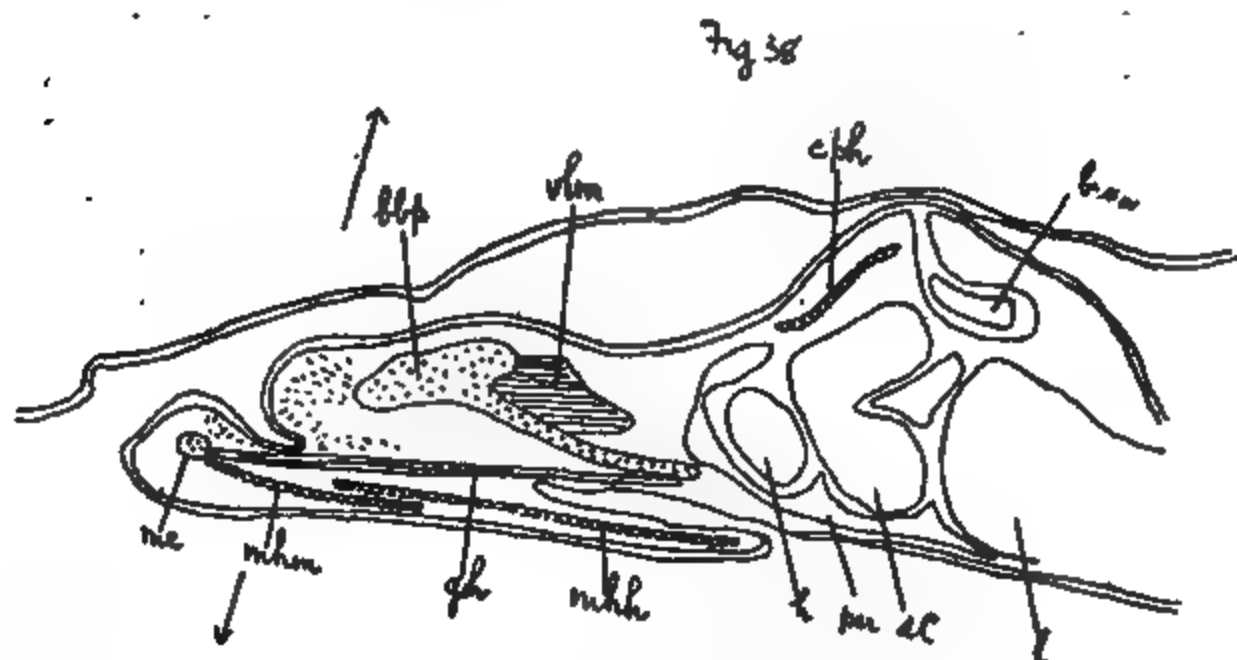


Elasmobranch body in front of the shoulder
shows much the same features as in the newt,
it, the trunk myotomes extend downwards, as
st,¹ between the parietal layer of peritoneum
from the whole of the muscles of the body wall,
transverse section (fig. 51) shows a picture quite
as seen in the newt (compare fig. 43).

valuable, and merits investigation, whether the
muscles of the trunk in the Sauropsida and
Amphibia are comparable in their formation those of Elasmobranchs
of Amphibia. The researches of Mall,² and
others, vol. xi.

² *Jour. of Morphology*, vol. xiv.

the strips are formed by the aggregation of cells from an undifferentiated or uniform sheet of mesoblast, and each divides into a dorsal—somatic—and a ventral—splanchnic—portion, in



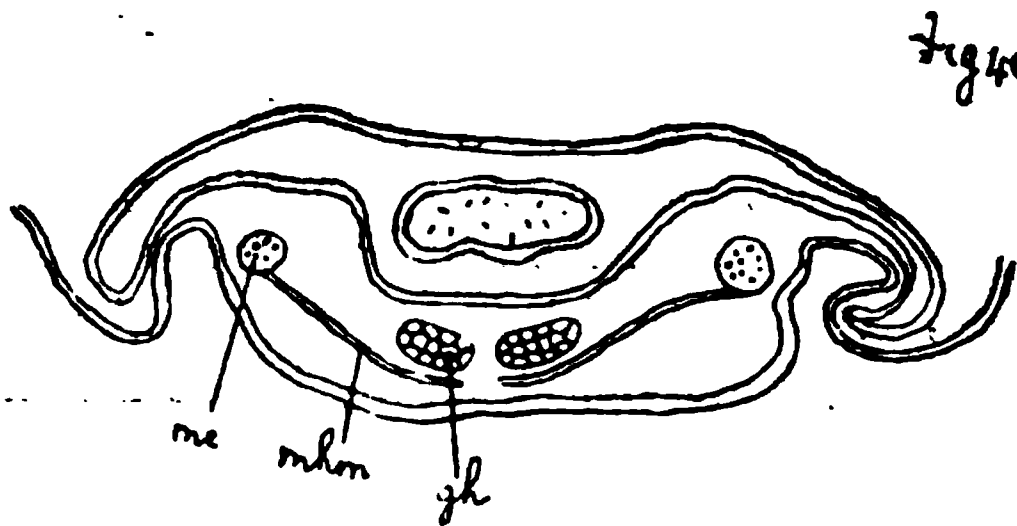
the newt they are formed by the conversion of the epithelial cells lining the upper and lower portions of the head cavities into muscle cells.

The muscle plates being formed in this diverse fashion in the

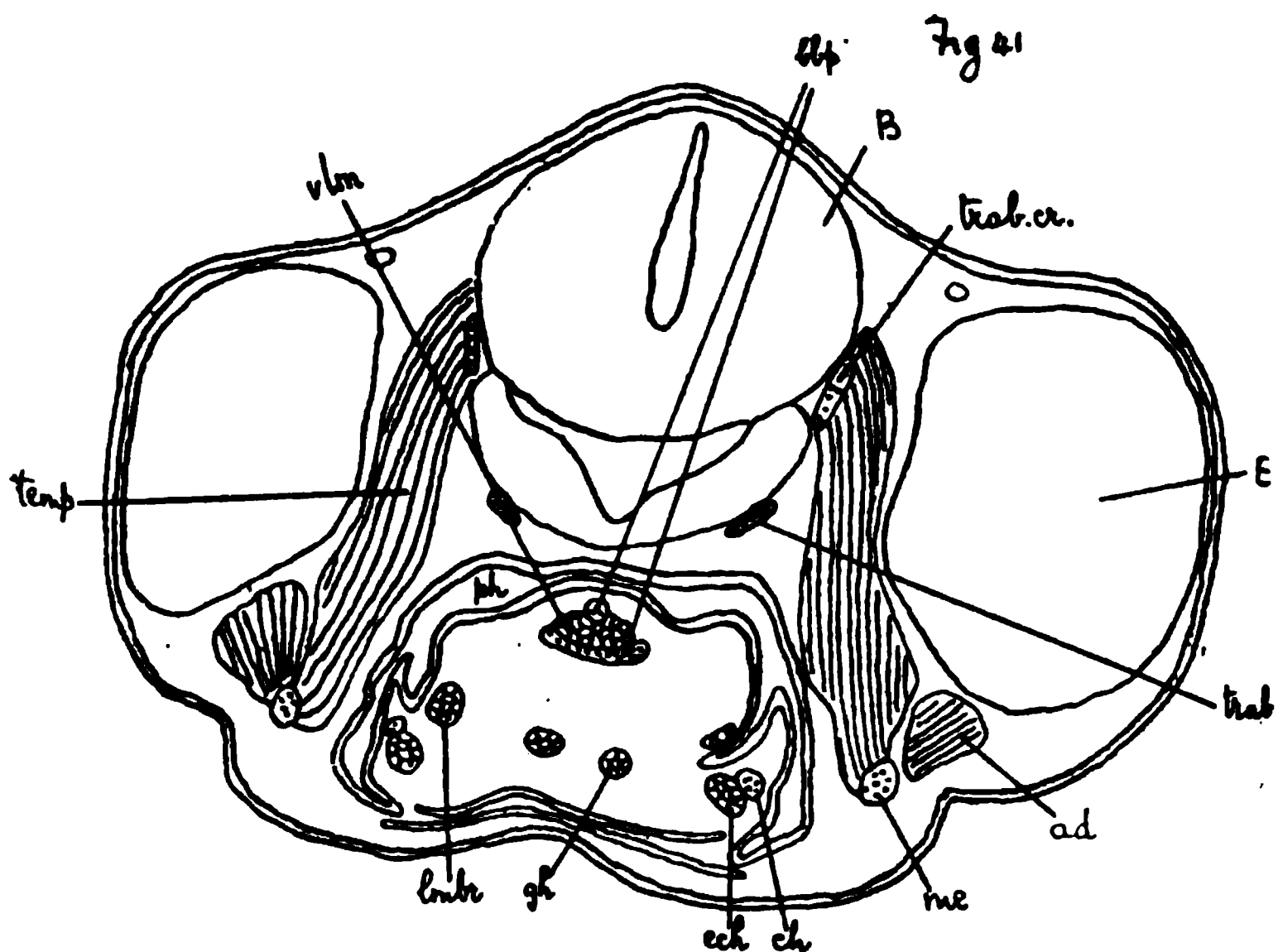
two animals, their development into muscles runs along closely parallel lines.

The splanchnic muscles may be taken first. The differences

are the following: In the toad, the meckelian and hyoidean mylohyoid form one continuous sheet, whereas in the newt they overlap. In the newt there is no submentalis. In both



animals the heart is developed in the 1st, 2nd, and 3rd branchial segments. The pharyngeal and laryngeal muscles, developed in the 4th branchial segments, are slightly different in the two



animals. In the toad, during the tadpole stage, there is no pharyngeal constrictor, and only the rudiments of the laryngeal muscles, which are attached on either side to the 4th branchial cartilage; at metamorphosis, a pharyngeal constrictor is

iii, iv, vi, and hypoglossal) innervate not merely muscles developed from myotomes, *e.g.*, the eye muscles and sterno-hyoid, but also muscles developed from visceral muscle plates, *e.g.*, the tongue muscles.

It is thus evident that in Amphibia the superficial origin from the central nervous system of the motor fibres innervating muscles developed in the head has no relation to the morphological position of the muscles they supply; and the dorsal position of the superficial origins of the motor fibres of the v, vii, ix, and x nerves, each of which innervates both somatic and visceral muscles, must have some other explanation.

Gaskell¹ states that "the point of vital importance in the estimation of the segmental value of the vertebrate cranial motor nerves is the arrangement of their central nuclei in the hind and mid brain." The nucleus of the abducens nerve, however, is posterior to that of the trigeminal, though innervating a muscle developed in an anterior segment. Again, the ventro-lateral muscles, though developed from head segments, are not, at least in the Ichthyopsida, supplied by cranial nerves. Further, the tongue muscles, though developed in cranial segments, are innervated by a nucleus which is spinal in position in Amphibia, medullary in position in Mammals.

It would seem probable, then, that the segmental value of the nuclei of the cranial nerves is to be determined rather by the morphological position of the muscles they innervate or 'represent' than by their arrangement in the mid and hind brain.

Representation of head muscle in the brain of the dog.—In the above mentioned paper I applied the results obtained from investigating the development of the head muscles in the toad, and the sizes of the motor nerve fibres to the head muscles in the dog, to revise the morphological value of some of their 'nuclei' in the cerebro-spinal axis.

The formation of the muscles in the newt's head makes matters a little clearer, and some further suggestions possible. In the newt's and toad's head there are three main series of somatic muscles, as described above. The middle set disappears in the toad with the assumption of an air-breathing condition,

¹ *This Journal*, vol. xxxiii.

and is totally unrepresented in the dog. The other two series of somatic muscles of the head are much alike in all three animals, the chief difference being that the elevators of the branchial arches (petrohyoids) are absent in the dog.

This is in marked contrast with the great development of the splanchnic musculature, with correlated neurons, in the head of the dog, as compared with these Amphibia.

It is possible, then, to classify the somatic 'nuclei' of the head segments of the dog into two series, innervating respectively dorso-lateral and ventro-lateral muscles.

Now, in the toad and newt it is remarkable that though the latter series of muscles are developed from head segments, their innervation is solely from the spinal cord. This holds, too, in the dog, with one possible exception, that of the geniohyoid; and this muscle, as previously suggested, may have its 'nucleus' in the most anterior part of the spinal cord, though its efferent fibres run out with the true, splanchnic, hypoglossal fibres.

The dorso-lateral muscles of the head, like those of the body, are innervated by nerve fibres which pass directly to each segment from corresponding ones in the cerebro-spinal axis.

The above described investigations thus lead to the following suggestions in regard to the head muscles of the dog:—

1. The motor nuclei in the mid and hind brain may be classified as follows: (*a*) *Somatic*, which innervate dorso-lateral muscles only. They are developed in the 1st, 2nd, 3rd, 4th (mandibular) and 5th (hyoid) segments only. (*β*) *Splanchnic*, which innervate muscles developed in the splanchnic region of the 4th, 5th, 6th, 7th, 8th, and 9th segments.

2. The ventral longitudinal muscles of the head and neck and possibly the ventro-lateral muscles of the trunk are developed from the ventral ends of the 7th, 8th, and 9th myotomes of the head. Their motor nuclei, however, with the possible exception of that of the geniohyoid, are spinal in position.

3. The chief contrast between the musculature of the head in the newt and dog lies in the great development in the latter of splanchnic—viz., facial, glossal, laryngeal, and pharyngeal—muscles; and there is a correlated development of splanchnic nuclei in the brain.

4. The hypoglossal nucleus, though innervating (splanchnic)

tongue muscles developed in the 4th and 5th segments of the head, is primarily spinal, and not medullary in position, and its intrusion into the medulla is probably due to its close association in function with other splanchnic pontal and medullary nuclei.

DESCRIPTION OF FIGURES IN TEXT.

[The outlines of the structures were drawn with a camera lucida, under a magnification of Zeiss, oc. 3, obj. A.]

Fig. 1. Stage 4, transverse section through mandibular segments. The hypoblast is here solid. The right side is a little posterior to the left, and passes through the hyomandibular cleft.

Fig. 2. Stage 4, transverse section through hyoid segment. The upper part of the segment is posterior to the lower, and the right side to the left.

Fig. 3. Stage 4, transverse section through 1st and 2nd branchial segment. The right side of the segment is anterior to the left.

Fig. 4. Stage 5, transverse section through mandibular segment. The right side of the section is a little posterior to the left.

Fig. 5. Stage 5, transverse section through hyoid segment. The right side of the section is a little posterior to the left.

Fig. 6. Stage 5, transverse section through 2nd branchial segment.

Fig. 7. Stage 5½, longitudinal vertical section.

Fig. 8. Stage 6, transverse section through mandibular and hyoid segments. The upper part of the section is more posterior than the lower, and the right side than the left.

Fig. 9. Stage 6, transverse section through 4th branchial segment. The right side of the section is more posterior than the left.

Figs. 10, 11, 12. Stage 6, longitudinal vertical sections. 10 is the most external.

Figs. 13-17. Stage 7, longitudinal vertical sections. 13 is the most external.

Figs. 18-22. Stage 7½, transverse vertical sections. 18 is the most anterior, the right side is more posterior than the left.

Figs. 23-33. Stage 8, longitudinal vertical sections. 23 is the most external.

Figs. 34, 35. Stage 9, longitudinal vertical sections. 34 is the most external.

Figs. 36-38. Stage 11, longitudinal vertical sections. 36 is the most external.

Fig. 39. Stage 13, longitudinal vertical sections.

Figs. 40-43. Stage 13, transverse vertical sections. 40 is the most anterior. The plane of fig. 40 is indicated by the arrows in fig. 38; it cuts through the projecting fold in front of the basibranchial plate.

Figs. 44-45. Stage 24, transverse vertical sections. 44 is the more anterior.

Fig. 46. Stage 24, longitudinal vertical section.

Fig. 47. Transverse section through tadpole of toad, just before metamorphosis, immediately behind the shoulder girdle. No ventro-lateral muscles are present. (From the same specimen as fig. 59, plate xix., *this Jour.*, vol. xxxiv.)

Fig. 48. Transverse section through tadpole of toad, during metamorphosis, immediately behind the shoulder girdle. Ventro-lateral muscles are now present. They can be traced back from the hind end of the ventral longitudinal muscles of the neck. (From the same specimen as fig. 71, plate xxi., *this Jour.*, vol. xxxiv.)

Fig. 49. Diagram of visceral skeleton and somatic muscles of head in a newt 9 mm. long. The position of the shoulder girdle (not developed until stage 11) is shown.

Fig. 50. Transverse section of a *Scyllium* embryo, stage M, just in front of the fore limb.

Fig. 51. Transverse section of a *Scyllium* embryo, stage M, behind the fore limb.

INDEX.

- A.* auditory vesicle.
a.d. anterior digastric.
B. brain.
b.a. mandibular tentacle or 'balancer.'
b.b.p. basibranchial plate.
br. 1. 1st branchial bar.
br. 2. 2nd branchial bar, etc.
br. 2, 3, and 4. united ventral ends of 2nd, 3rd, and 4th branchial bars.
bron. bronchus.
br.c. 1. 1st branchial cleft.
c.h. ceratohyal cartilage.
cor. coracoid.
c.ph. constrictor pharyngia.
d.C. ductus Cuvieri.
E. eye.
ec. ectoderm.
e.ch. external ceratohyal muscle.
e.g.br. 1. external gill of 1st branchial arch, etc.
e.m. eye muscles.
gg. genioglossus.
gh. geniohyoid.
h. heart.
hbs. hyobranchial cleft.
hs. hyomandibular cleft.
hy. hypoblast.
int. intestine.
l. liver.
lar. larynx.
l.m. limb muscles.
l.m.br. longitudinal muscles of branchial arches.
lx. lateral line branch of vagus.
m. 3. muscle plate of premandibular segment.
m. 4. muscle plate of 4th or mandibular segment, etc.
- m.md.* myotome of mandibular segment.
m.hy. myotome of hyoid segment.
m.br. 1. myotome of 1st branchial segment.
ma. masseter.
Me. Meckel's cartilage.
m.e.g.br. 1. muscles of external gill of 1st branchial arch, etc.
m.h.h. hyoidean mylohyoid.
m.hm. Meckelian mylohyoid.
N. nose.
n. notochord.
p.d. posterior digastric.
pel.gird. pelvic girdle.
per. pericardium.
pet.hy. 1. petrohyoid muscle of 1st branchial bar, etc.
ph. pharynx.
p.p.c. pleuro-peritoneal cavity.
S. suspensorium.
sh.gird. shoulder girdle.
so.s. stalk connecting the yolk sac with the embryo.
sp.c. spinal cord.
ster. sternum.
stom. stomach.
trab. trabecula.
trab.cr. trabecular crest.
th. thyroid gland.
temp. temporal.
tr.m. trunk myotome.
tr.m. 1. myotome of 1st trunk segment, etc.
v.l.m. ventral longitudinal muscles of neck and ventro-lateral muscles of trunk.

THE SEPARATE FUNCTIONS OF DIFFERENT PARTS
OF THE RIMA GLOTTIDIS. By W. A. AIKIN.
(PLATES X., XI.)

ONE of the difficulties attending the study of the normal action of the vocal organs is the rarity of good subjects for laryngoscopic examination. In laryngological practice it is not uncommon to meet with cases in which great toleration of the mirror in the fauces has been acquired by repeated examination, but a thorough examination of a normal larynx for physiological purposes is seldom to be got, and that only after patient exercise and training.

I have been exceptionally fortunate in this respect during the last few years, and have often been able to watch the movements of the larynx in trained voices with a large mirror and without protrusion of the tongue.

Several facts have thus come to my knowledge which do not appear to be recognised in the latest editions of standard physiological text-books, and which I now wish to put on record.

The anatomists have distinguished two divisions of the rima glottidis, to which have been given the physiological names of *Rima respiratoria* and *Rima vocalis*. It would be more strictly anatomical to describe them as *Rima cartilaginosa* (being formed by the vocal processes of the arytaenoids) and *Rima ligamentosa*, in accordance with their structures.

The rima ligamentosa should be divided physiologically into a short anterior portion, which is in contact during phonation, and not free to vibrate, and a vibratory portion, formed by the free margins of the ligaments which constitute the vocal reed, and may rightly be called the rima vocalis.

To give the rima cartilaginosa the physiological name of rima respiratoria is not entirely justified. During phonation, it is true, the respiratory function may continue through this part of the glottis, but during ordinary breathing the whole glottis is respiratory. It is more in accordance with the facts to call this

the glottic valve, as its function, during phonation, is to regulate the subglottic air-pressure by opening and closing.

Looking at a vertical mesial section of the larynx (Pl. X. fig. 1), the front part of the ligament, near its attachment to the thyroid cartilage, is seen to be thick, and may occupy as much as one-eighth of the rima. The length of the free margin of the ligament corresponds to about five-eighths, and the cartilaginous portion to about one-fourth, of the rima. The cartilage will be seen to spread out into a considerable triangular surface, as it extends backwards from the tip of the process.

The arytaenoideus muscle is inserted a little external to the angle where the base of the vocal process joins the rest of the arytaenoid cartilage, so that, when viewed from above, the corner of the cartilage is distinctly visible, forming the posterior limit of the rima (figs. 2-4).

These facts are of importance, because they remind us that in the laryngoscopic picture of the rima glottidis we must account for the whole length of the processus vocalis, then the free vibrating ligament, and in front of that the anterior attachment, and can then attribute to each its proper function.

Regarding this mesial section, it seems difficult to believe that there can ever have been any question as to the part of the rima glottidis which lends itself to the reed action of the voice. The fine elastic ligaments contrast so strongly with the thick cartilaginous wedges to which they are attached, that any thought of their being physically engaged in performing synchronous vibrations can only have arisen from the failure to distinguish which was which when viewing them from above. The physicist would be satisfied, on structural grounds alone, that the more or less sudden transition from the fine elastic tissue of the ligament to the denser cartilage of the processus vocalis would introduce a stop in the free vibration of the reed, apart from the fact that one presents a fine edge and the other a blunt wall. The distribution of fine powder, introduced experimentally, would afford no reason for altering this view.

I do not contend that the cartilaginous processes do not vibrate, for they must tremble when the vocal reed is in action; but I maintain that they are not involved in the vibration which produces the vocal note.

Of this I think there is abundant proof in the diagrams which are appended here. They were taken from the larynx of a trained singer of experience in the course of a long series of sittings, and the facts they illustrate have been verified again and again in the larynges of others and by other observers.

Figs. 2 and 4 show two positions of the glottic valve while singing the same note. In the former the valve is open, and in the latter closed. In fig. 3 is shown an intermediate position, in which the ligaments are fully approximated by the tips of the processes, but the posterior part of the valve is somewhat open. During the passage from one position to another, the vocal note continues without any alteration in pitch. When the valve is closed, the whole pressure of the breath is acting upon the reed, and the sound is more intense. When it is open, the subglottic pressure escapes and the intensity is diminished. The difference in quality need not be discussed here, but it is also characteristic.

What principally concerns the physiological side of the question is, that during the opening and closing of this valve the pitch of the vocal note remains unchanged, and that is a definite proof that the vibration is confined to the part of the glottis in front of the vocal processes, that is, to the free margins of the ligaments only.

When a very low note is being sung, the vocal ligaments are partly hidden by the epiglottis, but their edges, where visible, can be actually seen to vibrate while the glottic valve opens and closes with little or no tremor, and without changing the pitch of the note (figs. 5 and 6).

In the upper part of a man's voice, that is, from *c'* upwards, the open position becomes increasingly difficult, as the high pressure required for high notes escapes too readily through the opening. The intermediate position can be carried about a tone or so higher, but the tendency in singing is to use the closed position in the higher notes, for it is then easier to keep up the required pressure.

In figs. 7 and 8 are seen the positions of the glottis in the unnatural high notes of a male voice, or what has been called "falsetto." The ligaments are pressed together so firmly by the strong contraction of the lateral crico-arytænoid muscles, as well as the other muscles of approximation, that their edges are in

contact for a short distance in front of the vocal processes, leaving only a shortened length of ligament free to vibrate. It is possible to relax the arytenoidei muscles a very little, and allow a slight opening of the valve, without disturbing the pitch of the note.

It would take too long to go into the many practical questions involved in the regulation of subglottic air-pressure, but I need hardly point out its importance in training the voice. The free use of the valve is associated with a full development of the breath capacity, for it requires a larger volume of air in reserve. At the same time, it saves the vocal ligaments from undue compression, and consequent congestion, as shown by Dr Jobson Horne in some interesting photographs at the Ipswich meeting of the British Medical Association in 1900.

The glottic valve affords but one of our means of controlling subglottic pressure. The other is provided by the respiratory muscles. The action of these, assisted by the pulmonary elasticity, produces the positive pressure, and the valve then regulates the degree to which it shall affect the vocal reed. I have often met with misconceptions of this part of vocal physics, and think it cannot be insisted upon too clearly in physiological works that subglottic pressure is absolutely and entirely the source of vocal sound; that the elasticity of the vocal ligaments is only utilised to convert this into a rhythmically undulating air-stream; that the vibrations of the ligaments themselves are of importance only in so far as they affect the form of these undulations, and are otherwise practically inaudible; that the alternating rarefactions and condensations originate in the air by the action of the reed; and that all vibrations of solid structures may virtually be left out of consideration as sources of vocal sound in themselves.

I mention these physical facts in order to emphasise the importance of subglottic pressure, and the part played by the glottic valve in its regulation.

ON AN UNUSUAL FORM OF NASAL BONE IN A
HUMAN SKULL. By W. L. H. DUCKWORTH, M.A.,
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Anthropology.*

THE skull here represented (fig. 1) is that of an ancient Egyptian,
which was presented to the Anatomical Museum at Cambridge

FIG. 1.—Skull of ancient Egyptian, showing the unusually long nasal bone on
the left side. Notice particularly the line of foramina, which seem to denote
the original suture between the nasal bone proper and the uppermost part
of the premaxilla.

by Professor Petrie. The point to which attention is called is
the condition of the left nasal bone, which, as may be seen in
the figure, is prolonged downwards to an unusual extent along
the margin of the nasal aperture. The condition on the right
side is obscure, owing to the destruction of bone in this region;

the fragile nature of the specimen rendering it very liable to such injury.

Two explanations of the conformation of the left nasal bone appear to be possible. Thus it may be that ossification, commencing in the nasal bone, has spread to an unusual extent downwards into the superior lateral cartilage; the case would thus be regarded as one of an unusually large nasal bone.

Another explanation has been suggested by Professor Macalister. If the skull of a young gorilla be examined, it will be seen (as in fig. 2) that the premaxillary bones run

FIG. 2.—Skull of young gorilla (Camb. Anat. Mus.), showing the premaxillary bones extending upwards on the face till they meet the nasal bones.

upwards on the facial surface, skirting the lateral margin of the apertura pyriformis nasi, and meeting, at their highest parts, the nasal bones. The sutural lines are curiously persistent even in adult specimens of the gorilla, much more so than in the orang-utan, but a young example best shows the relations of the various bones.

It is suggested that such a relation of the premaxilla exists in the Egyptian skull under consideration, in which an

abnormally developed facial extension of the uppermost portion of the premaxilla has become fused with the nasal bone. It is very important to note that two or three small foramina seem to indicate the former situation of the line of junction. Without other examples, it does not seem possible to decide which of these explanations is the correct one; but the condition is rare enough in a human skull to render it worthy of being placed on record.

A NOTE ON IRREGULARITIES IN THE CONFORMATION OF THE POST-ORBITAL WALL IN SKULLS OF *HYLOBATES MULLERI*, AND OF AN ABORIGINAL NATIVE OF AUSTRALIA. By W. LAURENCE H. DUCKWORTH, M.A., *Jesus College, Cambridge*; *University Lecturer in Physical Anthropology.*

THE first example (fig. 1) is the skull of a specimen of *Hylobates mulleri*, presented to the Cambridge Anatomical Museum by

FIG. 1.—Skull of *Hylobates mulleri* (from the Anatomical Museum, Cambridge), showing a perforation in the post-orbital wall.

C. Hose, Sc.D., of Jesus College. In the outer wall of each orbit is a nearly circular aperture, most easily observed when the skull is viewed from behind.

The nature of such an imperfection in the orbital wall is of interest, in view of the well known generalisation that the completion of the partition between the orbit and the zygomatic

fossa is characteristic of the highest forms of Mammalia, and particularly of Primates.

In the genus *Hylobates*, the post-orbital wall is well developed normally, but the present example does not, in my opinion, exemplify a condition of retrogression or reversion on account of the imperfection alluded to; and this because the perforation is quite independent of the spheno-maxillary fissure, which is the last remnant of the communication between the orbit and

FIG. 2.—Skull of aboriginal Australian (No. 2163 in the Anatomical Museum, Cambridge), showing an unusually wide spheno-maxillary fissure.

the zygomatic fossa to be encroached upon by the more complete forms of septum; so that cases of reversion ought to present us with an abnormally wide spheno-maxillary fissure.

The perforations must therefore be regarded as due to defective ossification, similar to that which not uncommonly occurs in the infraspinous fossa of the scapula; no particular morphological significance can thus be attached to the condition.

The second example (fig. 2), which is the skull of an Australian aboriginal, does seem to bear evidence of an inferior type of conformation. As will be observed in the

photograph, the speno-maxillary fissure is of unusual width, the post-orbital wall being deficient in extent, though otherwise normally formed. There is thus an important difference between this condition and that exhibited by the skull of the gibbon first described, the deficiency in development of the post-orbital wall denoting an inferiority in the human skull. Another skull of an aboriginal Australian (No. 2126) in the same collection presents an almost identical condition.

Two remarks in conclusion seem to be appropriate. In the first place, when the members of the sub-order Lemuroidea (of the order Primates) are compared with those of the sub-order Anthropeidea, in respect of the outer portion of the orbit, it will be observed that the transition from the mere post-orbital bar of the Lemuroidea to the post-orbital wall of the Anthropeidea is a sudden one, and that in the lowest of the last-mentioned forms (Anthropeidea) the post-orbital wall is fully as well developed as in the Simiidæ. If, then, the Australian skull presents a condition of reversion, it is not a reversion to a lower stage among the Anthropeidea, but to a still more lowly form.

Secondly and lastly, when we compare normal examples of the highest Primates, such as the Simiidæ, with the Hominidæ, we find that, as a rule, the speno-maxillary fissure is still more nearly closed in the Simiidæ than in the Hominidæ, from which it seems justifiable to infer that *in this as in several other respects*, the Simiidæ have reached a further stage of development and specialisation than that attained by the Hominidæ. This consideration should certainly not be neglected in any summary of the evidence for the relative positions of members of the two families in question.

AN *ISCHIOPAGUS TRIPUS* (HUMAN), WITH SPECIAL
REFERENCE TO THE ANATOMY OF THE COM-
POSITE LIMB. By JAMES F. GEMMILL, M.A., M.D.
Lecturer in Embryology, University of Glasgow. (PLATES
XII., XIII.)

THROUGH the kindness of Professor Muir, I have recently had the opportunity of examining a full-time monstrosity of the above type, and in particular, of working out the anatomy of the composite limb, which happened to be extremely well developed and symmetrical. The results are given in the following paper, which also discusses some general points raised in the descriptive part.

The upper portions of the twin bodies are separate, there being two heads and two pairs of arms (Pl. XII. fig. 1). The pelves, the abdominal parietes and the lower parts of the sterna are united. Two of the legs are normal, forming a pair, but the third is composite and has ten digits, the great toes being adjacent. The extensor aspect of this limb looks away from the body of the monstrosity. The umbilicus and the cord are single. The twin bodies do not face each other quite squarely, but are slightly rotated towards the side which carries the pair of limbs and the umbilicus. The perineum is large and contains the orifices of a single centrally placed anus, of two vaginæ and of two urethræ. (Pl. XII. figs. 1 and 2.)

Measurements, etc.

From tip of coccyx to 7th cervical vertebra of each twin,	6½ ins.
Length of normal limbs from pubis to heel,	6½ "
„ composite limb from buttock fold to heel,	4 "
„ „ „ „ „ knee,	2 "
„ sole of composite foot,	2 "
Breadth of „ „ across bases of little toes,	1½ "
Circumference of composite limb at upper part of thigh, .	5 "
„ normal limbs „ „	4 "
„ composite limb just above heel,	3½ "
„ normal limbs „ „	2½ "

Circumference of the body at the pelvis,	12	ina.
Length of intestine of one of the twins from pylorus to place of union of intestines,	42	„
Length of intestine of the other twin from pylorus to place of union of intestines,	53	„
Length of intestines from place of union to cæcum,	12	„
Weight of the monstrosity (after removal of the liver),	7 $\frac{3}{4}$	lbs.

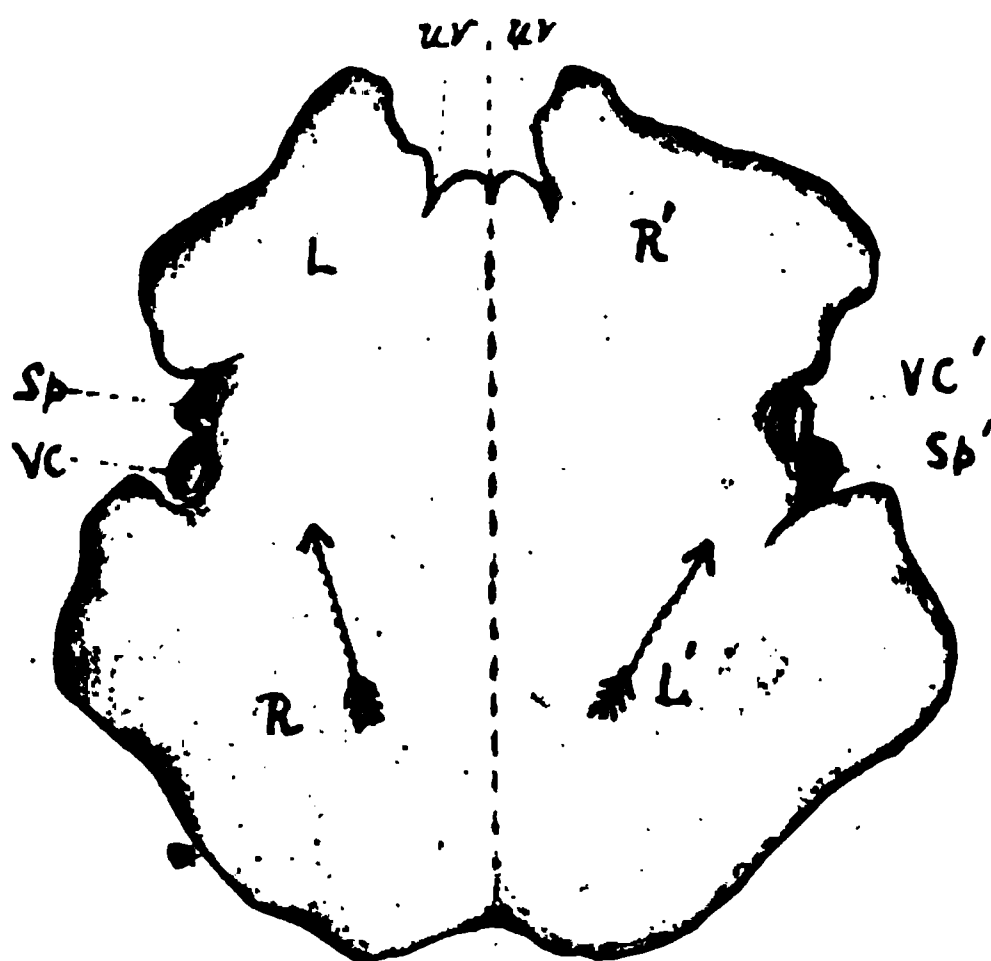
Viscera, etc.—The viscera are not transposed. The thoracic organs and cavities of each twin are separate and rest on a large composite diaphragm. (Pl. XIII. fig. 14.) The two pericardial sacs are in close apposition at the diaphragm, but towards their upper parts they become separated, following the diverging sterna. A large hernia projects upwards into the left pleural sac of one of the twins, carrying before it a delicate covering of diaphragm. It contains the whole of the stomach and spleen of the embryo to which it belongs, and is almost completely reducible. (Pl. XIII. fig. 14.)

The peritoneal cavity is single, but there is a separate stomach, duodenum, bile duct, spleen and pancreas for each twin. The small intestines unite a short distance above the ileo-colic valve. (For measurements see above.) No diverticula of Meckel could be made out. There is only one vermiform appendix, great intestine, and rectum. The great intestine has three well marked longitudinal muscular bands, but a fourth band is also present in its upper part.

The placental vein is single in the cord and at the umbilicus, but it bifurcates in the suspensory ligament on its way to the liver. This organ is composite and forms a large compact mass, roughly quadrate in shape as seen from above, and divided into four main lobes by as many fissures. Two of these lobes face the umbilicus and the fissure between them receives the two divisions of the umbilical vein, which pass one to each half of the composite mass and to the corresponding vena cava inferior. The remaining lobes are larger and are separated by a shallow fissure which contains only a mesenteric attachment. The inferior venæ cavæ of the two embryos produce the other two fissures, and these are situated directly opposite to one another. (See fig. p. 265.)

L and R indicate respectively the left and right lobes of the

half of the composite liver belonging to one twin, while R' and L' are on the right and left lobes belonging to the other twin. The two gall bladders are placed in fissures which lie symmetrically, one on the under surface of R and the other on the under surface of L'. Their positions are indicated by the arrows. It will be seen that L and R' resemble each other as regards form, size and relations to their respective umbilical veins. R and L', in turn, are similar in form and size and relations to the



Outline of the composite liver as seen from above. *u.v.*, *u.v'*, place of entrance of the two divisions of the umbilical vein; *v.c.*, *v.c'*, the two venæ cavæ inf.; *s.p.*, *s.p'*, the two Spigelian lobes. (Rest of explanation in text.)

gall bladders. All this indicates that many of the characters of R' and L' are *transposed*. But the transposition is not complete in every detail. For example, the Spigelian lobe, *sp'*, is placed, as in the normal liver, on the left of its corresponding vena cava, while the smaller markings on the under surface of L' do not correspond in all respects with those of R.

This *modified transposition* of characters in one half of the composite liver is all the more interesting because it is incomplete. It is present in that half of the liver which belongs to the twin embryo in which full transposition of viscera oftenest takes place in double monstrosities (*i.e.*, the left twin, as seen from the umbilicus). Though not complete, it simplifies the

relations of the umbilical veins and the gall bladders, and gives to the whole mass a general symmetry which is bilateral in the same plane as the symmetry of the composite pelvic organs to be afterwards described. This plane is at right angles to the sagittal planes of the embryos themselves.

Since the alimentary tracts are separate down to near the colon, two originally separate hepatic outgrowths must have united to form the composite liver, and this circumstance renders more striking the intimate character of their fusion and the general symmetry of the result.

Rectum.—The rectum is anchored in position by two mesorecta which pass outwards from its sides to the two sacra in such a way as to divide the lower part of the common pelvic cavity into two deep fossæ, each of which contains a uterus and bladder.

Kidneys.—Each twin has a pair of kidneys. These are normal as regards their form, position, and blood supply, and each of them is provided with a single ureter. (Pl. XII. fig. 8.)

Bladders.—There are two well formed urinary bladders (Pl. XII. fig. 8), which are situated on opposite sides of the composite pelvis, one behind each symphysis. The right ureter of one twin and the left ureter of the other twin go to one of the bladders, while, conversely, the other two ureters go to the second bladder. Each bladder has a pervious urethra and a urachus. The urachus on the side from which the umbilical cord arises is of the usual size and enters the cord, while the urachus on the opposite side is a thin fibrous thread, which loses itself in the abdominal parietes after passing upwards in the direction of an absent umbilicus.

Uteri.—Two uteri, with corresponding sets of broad ligaments and ovaries, are present, and are situated one between each of the bladders and the rectum. The uteri are bilocular and the vaginæ are double. There can be no doubt that each uterus is derived from Müllerian ducts which belong to different twins, and have not fully coalesced. Also, the ovaries in each pair belong to different twins.

External Genitals.—Adjacent to the normal symphysis, labia majora and minora have been developed (Pl. XII. fig. 2). The labia majora are truncated posteriorly and do not form a com-

missure behind the vagina. The labia minora are prominent, but the clitoris being absent, their anterior parts, instead of forming a hood for that organ, turn inwards to meet one another in front of the urethral opening. On the opposite side of the perineum (*i.e.*, adjacent to the composite limb) the external genitals are represented by a fleshy eminence, internal to which are the openings of the corresponding vagina and urethra.

Skeleton.

Sternum.—The sterna are separate above, but they unite at the level of the 4th rib cartilage. The united part bifurcates horizontally, and each of the resulting horns comes into connection with right and left rib cartilages, belonging to different twins.

Vertebral column.—The vertebral columns are separate along their whole length. Both sacra are sharply curved towards the side on which the pair of limbs is placed.

Pelvis.—The composite pelvis forms a single ring surrounding a large cavity. The right and left pubic bones of one twin come into connection respectively with left and right pubic bones belonging to the other twin, so that two symphyses are formed on opposite sides of the pelvic ring. One symphysis (that which is next to the normal pair of limbs) is normal in appearance, but at the other symphysis the whole of the arch from pubis to great ischial tuberosity is closely united with its neighbour, forming a large diamond-shaped plate, the upper and lower corners of which project markedly (Pl. XIII. fig. 9), and indicate respectively the fused pubic and ischial elements. The obturator spaces on this side are brought together, and are reduced to a single median triangular foramen (Pl. XIII. fig. 9, *Obt. F.*).

This foramen gives passage to a pair of obturator nerves and arteries, one of each coming from each twin. On the outer side of the fused ischio-pubic plate is a large articular cavity for the head of the composite femur.

The pair of limbs.—These limbs have the usual skeletal parts, with the usual pelvic and other muscles attached. It will be understood, however, that though they form a pair, they belong to different twins.

Bones of composite limb.—The femur (Pl. XII. figs. 3, 5), tibia (Pl. XII. fig. 6), astragalus (Pl. XIII. fig. 10), scaphoid, and the internal cuneiform are single composite pieces; the rest of the bones are doubled (Pl. XII. fig. 6; Pl. XIII. fig. 10).

Femur—(Pl. XII. figs. 3, 5).—The composite nature of the femur is indicated very definitely both by its form and by its muscular relations. It articulates, by means of a transversely expanded head, with the large cotyloid cavity previously mentioned (page 267). Its neck is short, and inclines upwards and backwards from the shaft. Below the neck, on the anterior aspect of the shaft, there is a prominent median crest with two lips which represent a pair of small trochanters (Pl. XII. fig. 3). The great trochanters are represented by two collar-like ridges, one on either side, just below the neck. Running down the middle line of the shaft in front is a ridge which is most strongly marked superiorly where it is continuous with the small trochanteric crest. The ridge in question gives attachment to several pairs of muscles, which will be referred to subsequently. On the posterior aspect of the shaft there are two well marked gluteal ridges beginning just below the neck and running down on either side of the middle line into lineæ asperæ. The two lineæ asperæ (Pl. XII. fig. 5, *La.*) come close together near the middle of the shaft, but diverge lower down.

The lower end of the composite femur carries four condylar eminences. The two outer condyles are of full size, but the two inner ones are small and closely united. Two anterior intercondylar grooves are present, one on either side, between each pair of inner and outer condyles. Each intercondylar groove is occupied by a patella (Pl. XII. fig. 3).

Tibia.—The tibia is composite, and the anterior surface of the shaft is subcutaneous (Pl. XII. fig. 6). The lateral aspects of the shaft give origin each to a tibialis anticus muscle and (in part) to an extensor longus digitorum. There are two interosseous edges, one opposite each fibula. The upper end of the tibia has two spines and four shallow articular depressions, corresponding with the four femoral condyles. The lower end projects markedly. At the ankle-joint there is great plantar flexion, so that the articular surface of the tibia, instead of being horizontal, looks downwards and backwards.

Fibulae.—Two fibulae are present, one on either side of the tibia (Pl. XII. fig. 6). They are placed a little further back than normal, especially at their upper ends.

Astragalus.—(Pl. XIII. fig. 10).—The large composite astragalus articulates superiorly, by means of a single joint, with the tibia and the two fibulae. It also articulates anteriorly with the single scaphoid, and inferiorly with the two calcanea, to each of which it is connected by the usual interosseous ligament.

Calcanea.—The two calcanea take up slightly everted positions underneath the astragalus, one on either side of the middle line of the composite foot. Close under the astragalus their sustentacula tali articulate with one another by means of a synovial cavity, which is continuous with that of the astragalo-calcaneo-navicular articulation. The calcaneal tuberosities are very firmly connected with one another by transverse ligaments across the middle line of the composite foot.

Scaphoid.—The large shallow composite scaphoid articulates in front with the five cuneiform bones. At its outer angles there are small facets for the adjacent corners of the cuboids. (See Pl. XIII. fig. 10.)

Internal cuneiform, metatarsals, etc.—The internal cuneiform is composite. So also is the first metatarsal. The joint between these two bones is deeply concave, the concavity looking forwards.

The cuboids, the middle and outer cuneiforms and the four outer metatarsals and their phalanges form a double set (Pl. XIII. fig. 10).

The second metatarsals at their bases are separated from the first metatarsals by a comparatively wide interval.

A small median extra piece of cartilage articulates by a synovial cavity with the distal end of the composite metatarsal, and receives slips from the extensor tendons of the hallux.

Great toes.—The great toes are separate, and each has a set of three phalangeal pieces. The proximal elements in each set are connected by fibrous union with the sides of the composite first metatarsal near its distal end, but proper synovial cavities are present at the articulations between the pieces themselves. Probably the two terminal elements in each set alone represent true great-toe phalanges.

Ligaments.

Sciatic ligaments.—The great and small sciatic ligaments are reduced in thickness, but as the pelvic ring is much widened, their other dimensions are greatly increased, especially on the side which carries the composite limb. As was indicated previously, sacrum and coccyx are turned away from this side.

Hip-joint ligaments.—The capsule of the hip-joint of the composite limb is very strong in front, but very weak posteriorly. There is no proper ligamentum teres, but in the middle line of the joint anteriorly a thickened part of the capsule projects inwards as a prominent fold the attachments of which encroach a little on the articular surfaces of femur and innominate bone. Probably this fold represents the fused round ligaments.

Knee-joint of composite limb. — Unfortunately, this joint, which had been torn open at birth, was too much damaged for accurate dissection. But it could be made out that the joint was completely divided into two halves by a median antero-posterior septum. Within each half were an inner and an outer condyle from the composite femur, a pair of semilunar cartilages, and a reduced tibial spine. The common tendon of the graciles and sartorii muscles passes over the front of the joint. Each of the two intercondylar grooves has a corresponding patella.

Interosseous membrane.—Interosseous membranes are present between the fibulæ and the tibial edges adjacent to them.

Ankle-joint and Foot.—Over the front of the ankle-joint, the prominent lower end of the tibia is connected firmly with the astragalus and scaphoid by means of three ligaments, one of which is median, while the other two are placed at its sides. The ankle-joint is composite, and the ligaments in question represent the anterior and middle bands of a pair of internal lateral ligaments.

Posteriorly, the lower ends of the tibia and fibulæ are connected with the astragalus and with the calcanea by strong decussating bands of fibres, which are to be looked upon as representing a pair of external lateral ligaments.

The plantar fascia will be referred to later. The inferior calcaneo-navicular ligaments decussate very strikingly on either

side, and the calcaneal tuberosities are bound together across the middle line by strong transverse fibres.

Muscles, etc.

Corresponding to the two symphyses pubis in the monstrosity are two abdominal regions, the walls of which contain the usual fasciæ and muscles. These regions are bounded superiorly by one or other of the horns of the bifid sternum and by the adjacent lower ribs. It will readily be seen that, as in the case of the pelvis, these regions have composite walls. For example, in each of the two pairs of rectus abdominis muscles, one rectus belongs to one of the twins, while the other rectus belongs to the other twin. The same thing is true for the other muscles and fasciæ. Each of the two hypogastric regions contains the usual diverticula of Nück, leading downwards from inguinal canals, and containing round ligaments. There are thus two pairs of these structures. It will be seen afterwards that two quite separate uteri are present.

The abdominal wall on the side which carries the normal limbs has a normal umbilicus and an umbilical cord, but the abdominal wall on the side which carries the composite limb has no trace even of an umbilical scar.

Pelvic muscles.—Each of the twins has a complete set of pelvic muscles. These muscles are rearranged to suit the altered relations of the skeletal parts to which they are attached.

Perineal muscles, etc.—(See Pl. XII. fig. 4).—The levators of the anus belonging to either twin meet at a fibrous raphé, which extends from the tip of the coccyx inwards to the anus. Here they spread out, and serve to support the rectum, vaginæ and bladders. In so doing they come into connection with such of the other perineal muscles as are present.

On the side from which the sacra are turned away, the ischio-rectal spaces are too shallow to form fossæ. Accordingly, the corresponding levators of the anus and the coccygeal muscles appear as greatly expanded subcutaneous sheets, while the corresponding pudic nerves are also subcutaneous. The levators of the anus, which have just been mentioned, arise close together from the inner aspect of the fused ischio-pubic plate, below the places of origin of the internal obturators. On the opposite side

of the pelvis, where the symphysis is normal, the two levators of the anus have their usual origins.

From each of the normal ischial tuberosities, and from the ramus in front of it, a fan-like sheet of muscle fibres passes inwards to support the orifice of the corresponding vagina and urethra, and decussates with fibres of the levators of the anus. In the absence of a definite triangular ligament or of a clitoris, this sheet (which is not subdivided) may be considered to represent superficial and deep transverse muscles of the perineum, with, perhaps, remains of the constrictor vagina and erector clitoridis.

From the fused ischial tuberosities on the opposite side two small muscles pass inwards towards the adjacent urethra and vagina, and blend with the neighbouring levators of the anus. In all probability they represent a pair of transversus perinei muscles.

Limb muscles.—The pelvic muscles going to the two normal limbs are normal, but it will be understood that the two sets belong to different twins.

Muscles arising from Pelvis, and attached to Composite Femur.

Ilio-psoas.—Two ilio-psoas muscles (one from each twin) converge as they pass downwards over the brim of the pelvis, and are inserted from either side into the crest representing the fused small trochanters. Similarly, the mesial ridge running from this crest down the front of the femur gives attachment from above downwards to two pectinei muscles, two short adductors, and two long adductors. The insertion of each pair is V-shaped. The two limbs of the V inclose the pointed apex of the next muscular insertion as one goes upwards in the series.

Gluteal muscles.—Each twin has full sets of gluteal muscles, all of which have the usual pelvic origin. The two g. maximi which pass to the composite limb are inserted into the gluteal ridges of the composite femur (Pl. XIII. fig. 11); the g. medii are inserted on the outer aspect of the great trochanter eminences, one on either side, while the g. minimi are inserted into the same eminences more anteriorly.

Obturator muscles, etc.—Two small internal obturator muscles

arise from the pelvic aspect of the ischio-pubic plate, behind the obturator foramen (Pl. XII. fig. 5, *Gl. R.*). After leaving the pelvis, they are inserted, along with the pyriformes, into the great trochanter eminences of the composite femur. The pyriformes are much reduced in size. Gemelli and quadratus femoris muscles cannot be made out. The external obturators are represented by two small muscles which arise from the outer aspect of the ischio-pubic plate below the cotyloid cavity and are inserted side by side into the groove which separates the head of the composite femur from its neck posteriorly. The adductor magnus is separated altogether from the other adductors, and lies at the back of the composite limb. There it is represented by a considerable mass of muscle, arising above from the outside of the ischio-pubic plate behind the cotyloid cavity, and inserted below into the inner lips of the two lineæ asperæ and into the intervening surface on the femur. This mass can only represent fused adductor magnus muscles. It is innervated by branches from the great sciatic nerves on either side.

Hamstring muscles.—The semitendinosus and semimembranosus are absent, but two large biceps muscles arise close to one another from the fused ischial tuberosities. Their fibres decussate near their origin. The muscles then separate, and each, after receiving a deep head from the linea aspera on its side, passes down to be inserted into the head of the fibula. They form the upper boundaries of the popliteal space on the back of the composite limb.

Quadriceps muscles.—There are two sets of quadriceps extensor muscles covering the surfaces of the femur which lie on either side between the median anterior ridge and the lineæ asperæ. (See figs. 3 and 5, Pl. XII.; also figs. 11 and 12, Pl. XIII.) The quadriceps tendons are inserted each into a patella and then into the head of the tibia, some distance outwards from the middle line in front. (See figs. 3 and 6, Pl. XII.) The recti arise from the anterior inferior spines, and have no reflected heads. The relations of the vasti and the crureus in each set are normal.

Gracilis.—Two gracilis muscles arise, one on either side of the middle line, from the outer aspect of the symphysis pubis, near its summit, and pass side by side down the middle of the front

of the thigh, superficial to all the other muscles. Their tendons unite some distance above the knee-joint; and after being joined on either side by the tendons of the sartorius muscles, they pass in front of the knee-joint, to be inserted in the middle line into the front of the head of the tibia. (See fig. 3, Pl. XII)

Sartorius.—The sartorius and tensor vaginæ femoris muscles on each side are apparently united in one mass, which is innervated both from the anterior crural and the gluteal nerves. The tendon joins that of the gracilis muscles in the manner just described.

Muscles of leg.—There are two full sets of peroneal and anterior leg muscles in the composite limb, but the posterior muscles are only imperfectly doubled.

Tibialis anticus.—These muscles are large, and they arise from the lateral surfaces of the composite tibia. Their tendons lie in shallow grooves on the sides of the lower end of the tibia, and, converging as they cross the ankle-joint, they unite over the composite scaphoid. The common tendon is inserted into the dorsal aspect of the internal cuneiform, and partly also into the base of the 1st metatarsal.

Extensor hallucis.—These muscles are reduced in size. The tendons emerge below the ankle-joint, just outside those of the tibialis anticus. Opposite the middle of the metatarsus, each divides into an inner and an outer slip. The inner slips are continued on to the small extra cartilaginous piece at the distal end of the first metatarsal. The outer slips go to the dorsum of the great toes, and are joined by tendons from the short extensors of the toes.

Extensor longus digitorum.—The extensor longus digitorum muscles on either side are quite normal, except that their tendons, as they pass through the anterior annular ligament, suffer an outward instead of an inward change of direction.

Peronei.—Peroneus longus and brevis on either side are normal, except that the tendons of the first, after crossing the sole obliquely from opposite sides, are inserted together into a small cartilaginous piece articulated to the plantar side of the proximal end of the 1st metatarsal.

There are no third peronei muscles.

Extensor brevis.—On each half of the dorsum of the foot

there is an extensor brevis muscle with four tendons. The origin and insertions are normal.

Gastrocnemius.—There are two gastrocnemius muscles, the sheaths of which are connected by fibrous tissues across the middle line. The outer bellies alone are represented. Each arises by a single head from above the outer condyle of the composite femur on its own side, and each passes downwards to be joined by a soleus tendon, and to be inserted into its corresponding calcaneum.

Soleus.—Two soleus muscles are present, but each arises only from its corresponding fibula. Their sheaths are connected by fibrous tissue.

The plantaris longus is absent. So also are the flexor longus hallucis and the tibialis posticus.

Flexor longus digitorum.—Two long flexor muscles of the toes are present. They arise from the middle two-thirds of the shaft of each fibula. Their tendons pass into the sole of the foot between the two calcanea. Before dividing into digital slips, each tendon expands into a broad flat band. The two bands are connected with one another for some distance by a stout fibrous sheet, on the surface of which there are distinct muscle fibres. The digital slips go to the four outer toes on either side.

Plantar fascia.—A strong sheet of this fascia arises behind from each of the two calcaneal tuberosities. The two sheets decussate very markedly across the middle line, and end by dividing into the usual digital slips.

Flexor brevis.—There are two flexor brevis digitorum muscles, one arising from each of the two calcaneal tuberosities. They decussate almost completely to opposite sides, one of them passing superficial to the other.

Flexor accessorius. — The flexor accessorius muscles are separate, each being in connection with its proper flexor longus tendon.

The lumbricales and interossei muscles and the muscles of the little toes are normal.

The abductors of the hallux are wanting.

The short flexors of the hallux are present and are quite separate from one another, but each has only a single head of

origin. They are inserted partly into the cartilaginous piece at the distal end of the first metatarsal, and partly into the hallux itself on either side. An adductor hallucis and a transversus pedis are present on either side. They are inserted mainly into the terminal cartilage just mentioned.

Vessels.

The umbilical vessels and the vessels of the composite limb and pelvis alone require description. The rest of the vascular system in each embryo is normal.

The aortæ in the twin embryos are quite separate from one another. Each aorta divides unequally into a right and a left common iliac. The right common iliac of one twin is much larger than the left, while the left common iliac of the other twin is much larger than the right.

The two larger common iliacs divide into external and internal iliacs, of which the first are continued as femoral arteries to the pair of normal limbs, while the internal iliacs supply the adjacent pelvic parts and give off the umbilical arteries. Thus the umbilical arteries are two in number, and belong to different embryos.

The two smaller common iliacs supply the composite limb and the adjacent pelvic parts. Each divides into an external and an internal iliac. The two external iliacs, after passing over the brim of the pelvis, one on either side of the compressed symphysis, are distributed as femoral arteries to the muscles, etc. on the front of the thigh in the composite limb, but they do not reach lower than the knee.

The two internal iliacs in this set divide into the usual pelvic branches, but the following points deserve to be noted :—

(1) No umbilical arteries, whether pervious or obliterated, arise from them.

(2) The lateral sacrals are larger than normal, being distributed to the convex sides of the curved sacra.

(3) The obturator arteries are very minute.

(4) The sciatic arteries are much enlarged. They leave the pelvis between the lumbo-sacral cord and the first sacral nerve root, emerge below the pyriformis at a level deeper than that of

the great sciatic nerve, and, after giving off muscular and other branches, are continued downwards to the popliteal space on the back of the composite thigh. Here they unite with one another, and the common trunk, after giving off articular and sural branches, is continued down the back of the leg, beneath the adjacent edges of the solei muscles. Various muscular and two anterior tibial arteries are given off unsymmetrically in the upper part of the leg. Opposite the middle of the leg the common trunk divides into two branches, both of which run downwards in the middle line, the one being placed at a deeper level than the other. The more superficial branch, which is also the larger, will be seen to correspond to fused posterior tibials; the deeper branch does not seem to have any homologue in normal anatomy. Just above the ankle-joint the former (*i.e.*, the posterior tibial artery) divides into a small median and two larger lateral branches. At this part the artery is lying behind the fused posterior tibial nerve, to be afterwards described. The median branch of artery perforates the nerve, and is continued down the middle of the sole of the composite foot, accompanied by a median plantar branch of nerve. This median artery obviously corresponds to a pair of fused internal plantars, while the other two divisions of the posterior tibial correspond to external plantars. They pass outwards, one on either side of the sole of the composite foot, in company with external plantar nerves, and each forms a plantar arch of its own.

The large deep branch of artery which was mentioned above as being given off in the leg, lies at first close against the muscle fibres which decussate from the tibia to the fibulæ. Lower down, it rests on the tibia itself. After giving off articular branches at the ankle-joint, it passes into the foot through the bottom of the cleft between the two calcaneal tuberosities, deeper than all the other soft structures and resting on the capsule of the joint, between the adjacent sustentacula tali. It then passes forwards on the plantar side of the composite scaphoid, internal cuneiform and 1st metatarsal bones, giving off branches on either side and becoming gradually smaller.

Nerves.

The two pairs of lumbar and sacral plexuses are normal in their essential features, but the courses of many of their roots and branches are modified, especially on the side which carries the composite limb.

Pudic nerves.—Mention has already been made of the subcutaneous position of the two pudic nerves on this side, in the absence of ischio-rectal fossæ. Owing to the great rearrangement of parts, the distribution of the pudic nerves is far from being typical. Branches could be traced only to the sides of the anus and vagina adjacent to the place of emergence of each nerve.

Obturator nerves.—The obturator nerves on the side which carries the composite limb, pass with their corresponding arteries through the small single obturator foramen, and are distributed to the graciles, the long adductors, the short adductors and the pectinei muscles. These last are innervated in addition by the anterior crurals. The adductor magnus gets its nerve supply entirely from the great sciatic nerves.

Great sciatics.—The two great sciatic nerves (fig. 7, Pl. XII.) divide high up into external and internal popliteals. The external popliteals curve round the necks of the two fibulæ, and divide into musculo-cutaneous and anterior tibial branches, which are distributed to the two sets of peroneal and anterior leg muscles, and to the two halves of the dorsum of the composite foot. The chief part of each external saphenous nerve is supplied by the external popliteals.

Digital nerves.—The following is the arrangement of the digital nerves in each half of the dorsum of the foot:—The external saphenous supplies both sides of the little toe and the fourth toe, as well as the outer side of the third toe. The musculo-cutaneous supplies (*a*) adjacent sides of the second and third toes, (*b*) the inner side of the great toe; the anterior tibial supplies adjacent sides of the first and second toes. It will be seen that this arrangement differs somewhat from the usual. As a rule, the external saphenous nerve supplies only the outer aspect of the little toe.

The internal popliteal nerves (fig. 7, Pl. XII.), like the arteries

accompanying them, unite opposite the lower end of the femur, and the single trunk, after giving off articular and sural branches, and two very slender tibial communicating branches for the external saphenous nerves, is continued down the back of the leg superficial to the artery.

Posterior tibial, etc.—Some distance above the ankle-joint it gives off a branch on either side for the flexor longus digitorum, and lower down a calcaneo-plantar branch. Just above the ankle-joint it is perforated by the median artery mentioned above as representing the fused internal plantar arteries. At the same level it divides into a large median and two smaller lateral branches. The lateral branches correspond to external plantar nerves. They supply digital nerves for the little toes and the outer sides of the fourth toes, besides giving off the usual deep branches. The median division corresponds to fused internal plantar nerves, and its digital branches, which supply the rest of the toes, are given off in the following manner:—Before the middle of the sole is reached, a branch comes off on either side, which, after subdividing, is distributed to adjacent sides of the little, fourth and third toes. Further forwards, another branch is given off on either side, which, after subdividing, is distributed to adjacent sides of the third, second and great toes. The slender continuation of the median trunk passes forwards to supply the plantar aspect of the fused metatarsal and the cartilage at its extremity, as well as the inner sides of the two great toes.

(A drawing of the vessels and nerves is given in fig. 7, Pl. XII.)

GENERAL.

As the anatomy of the skeleton and viscera of a considerable number of ischiopagi has already been collated by various authors, in particular by Taruffi (*Storia della Teratologia*, vol. ii. pages 366–403), I have thought it superfluous to enumerate the points in which my specimen agrees with or differs from others previously described. But it may not be out of place to refer to some general considerations suggested by the descriptive part of this paper.

It has been seen that the composite pelvis contains a double

set of parietal as well as of visceral structures, excepting only the great intestine and rectum which are single. All the parts which are paired in normal anatomy have been so rearranged that in this monstrosity each pair consists of elements from different embryos. This is true for the derivatives of the Müllerian ducts (tubes, uteri, and vaginae), for the ovaries and for the ligaments, as well as for the pelvic vessels and nerves, the pelvic and abdominal parietes and the perineal muscles.

The two bladders cannot, however, be looked upon as having been produced by the secondary union of halves belonging to either embryo. They show no trace of duplicity either on their external or on their internal aspect, and each is continued upwards into a single urachus cord. This condition is all the more striking inasmuch as the cavities of the paired Müllerian ducts have remained separate in each of the uteri, in spite of the fact that the ducts in question are situated close to the common rectum, and in spite of the tendency to fusion which every pair of Müllerian ducts exhibits in normal development. There can be no doubt that in this monstrosity two allantoic diverticula grew out in opposite directions from opposite sides of the composite cloaca.

Their plane of growth was at right angles to the sagittal planes of the twin embryos, and this deviation may be set down to the influence of neighbouring structures. When the allantoic diverticula began to be formed, the composite pelvis would be taking shape round the common cloaca, the parietes would contain blastema from different embryos, and Wolffian ducts of similar origin would be associated together at their openings into the cloaca. The influence of all these rearrangements might well, through correlation of growth, induce the formation of two allantoic diverticula, and direct them towards the two new middle lines of the abdominal parietes. Besides, the allantoic blastema of the cloaca may itself have been placed from the first in these new positions. Anyhow, it is clear that the bladders are not the result of fusion of outgrowths, but were single from the first.

The Composite Limb.

As regards the origin of the limb, everything indicates that

it developed as a composite structure from the first, being occasioned by the overlapping of the spheres of influence and tissue formation of the twin embryos. Different tissues are, however, united in different degrees, and in particular the mesenchymal and muscular groups stand in marked contrast in this respect. (See page 282, where an explanation is given.)

One can infer that the growth and differentiation of the limb took place under the influence of (1) a tendency on the part of the blastema to develop two full sets of structures, and (2) a controlling influence which served to mould the double set of structures into a shapely organ. The composite limb, taken as a whole, or with reference to any of its parts (hip-, knee- and ankle-joints, etc.), cannot but strike one as being a remarkably good result. In this connection the foot is particularly interesting, because, in addition to mere union and compromise, there is a definite rearrangement of structures, and more than that, a development of new structures for purposes of mechanical support. The transverse arch of this foot is of double width, as it is formed from two arches placed side by side, so that the composite scaphoids and internal cuneiforms are in the position of keystones. If nothing more than union of adjacent structures had taken place in the development of the foot, this arch would have been very inadequately braced up, and would have been all the weaker for its great width. But, as a matter of fact, one finds that a great many muscular and fibrous structures are rearranged in such a way as to brace up the arch. The two plantar fasciæ and the two sets of short flexors of the toes decussate completely from side to side; the tendons of the long flexors of the toes are joined together across the middle line in the sole by a broad ligamentous band which has muscle fibres on its surface, and would give the effect of decussation, especially if conjoined with action of the flexor accessorius muscles. Also, the inferior calcaneo-navicular ligaments are very strong, and decussate very markedly, while the two calcaneal tuberosities are bound together by strong transverse fibres. It looks as if nature had tried to make the composite foot a mechanically good one, in anticipation of its future possible use; and it is worthy of note that on the dorsum of the foot (*i.e.*, the convex

L' corresponds to *L* in fig. A, and the half circle on which it is placed corresponds to the full section to which *L* points in fig. A. Conversely for *R'* and *R*.

A A are now widely separated from *P P*, being placed on the opposite sides of the composite limb.

The rearrangement of parts in the composite leg and foot may be explained by reference to planes of separation similar to that which has just been described for the thigh. These planes should cut the skeletal parts on homologous aspects. This means that the linea aspera of the femur (between its lips) corresponds to the inner border of the tibia, and to the internal aspect of the inner set of foot and ankle bones. This inference is in harmony with the view that the shaft of the femur undergoes an inward rotation during normal development.

Very few structures have been crowded out of the composite limb. Double sets of all the normal vessels and nerves are present, except in the case of certain trunks which have fused together. Several muscles, however, are not represented. Most conspicuous by their absence are the semitendinosus and semimembranosus, the flexor longus hallucis and the tibialis posticus. There is absence also of the gemelli, the quadratus femoris, the inner belly of each gastrocnemius, and the abductor and opponens hallucis.

New structures, etc.—Of entirely new structures or relations present in the composite limb, the most interesting set occurs on the plantar aspect of the foot, and has been referred to above. The muscles which decussate from the tibia to the fibulæ, and the extra cartilaginous pieces in connection with the first metatarsal bone deserve also to be mentioned here.

Arteries.—In the composite limb the sciatic arteries take the place of femorals in supplying the leg and foot. The true femorals are small, and stop short above the knee, their further course being barred on account of the union of the femora. It is interesting to note that the posterior tibial and plantar arteries, though derived from the sciatics of the composite limb, are distributed in a manner which corresponds on the whole to that of normal vessels.

Muscles.—The twin sets of muscles in the composite limb show a remarkable tendency to remain separate. They may unite by their sheaths (gastrocnemius, soleus, etc.) or by their tendons (gracilis, sartorius), but the only example of union of actual muscular tissue is found in the (reduced) adductor magnus.

Connective tissues.—On the other hand, the skeletal and con-

nective tissues exhibit the greatest tendency towards union. The single condition of the femur, for example, contrasts very markedly with the double set of muscles in the thigh, and is all the more striking on account of the central position of the femur itself. The circumstance seemed very remarkable to me on comparing it with the behaviour of the axial skeleton of the body in a large series of double monster trout embryos which I examined lately. There, the notochords and the vertebral cartilages remained double longer than any other structures, and, in particular, long after the adjacent muscle masses had united intimately. The contrast can be explained developmentally. The diffuse and partly peripheral origin of connective tissue will facilitate a ready union of mesenchyma in any part of a developing double monstrosity where overlapping of embryonic areas takes place, as, for example, in a composite limb bud; but in such a bud the muscular tissues, which have a more definite and central origin (the mesoblastic somites), will tend to remain separate. On the other hand, in double monsters with united axes (*e.g.*, the trout embryos above mentioned), the adjacent mesoblastic somites at the angle of convergence of the axes will naturally come together earlier than the notochord. The double condition of the muscles in the composite limb does not, accordingly, depend on any idiosyncrasy of muscular tissue as a tissue, but on its mode of origin.

Nerves, etc.—The nerves and blood-vessels of the composite limb are, no doubt, in whole or in part, centrifugal in development, and their union in the back of the leg and the foot is to be explained as a union of the connective tissue in their sheaths and walls.

EXPLANATION OF PLATES.

PLATE XII.

Fig. 1. Sketch of the monstrosity, as seen from the side which carries the composite limb.

Fig. 2. Perineum, etc., of the monstrosity, showing the pair of normal limbs with external genitals between them, the centrally placed anus and the composite limb. The external genitals on the side

which carries the composite limb are represented by a fleshy eminence lying external to the openings of the corresponding urethra and vagina.

Fig. 3. Front view of composite femur and head of composite tibia, showing attachments of muscles.

- Art.* articular surface of femur at hip-joint.
- L.T.* round ligament.
- Gt. Tr.* great trochanter on one side.
- Il. ps.* V-shaped insertion of the two ilio-psoas muscles.
- Pect.* " " " pectinei "
- Add. br.* " " " short adductors.
- V.I.* boundary line of origin of vastus internus on one side.
- Add. l.* V-shaped insertion of the two long adductors.
- Sart.* tendon of the sartorius on one side.
- Gr.* fused tendon of the graciles muscles.
- I. Gr.* intercondylar groove on one side.
- Q.E.T.* quadriceps extensor tendon.
- Pat.* patella.
- L. Pat.* ligamentum patellæ.

Fig. 4. Dissection of muscles, etc. of perineum of monstrosity.

- 1.1'. placed on either side of the anus, on the raphé between the levators of the anus.
- 2.2'. levators of the anus.
- 4.4'. the fan-shaped sheet of muscle representing fused perineal muscles (page 272).
- 4a. transversus perinei (page 272).
- 5.5'. coccygei muscles.
- 6.6'. great sacro-sciatic ligaments.
- 7.7'. tuberosities of ischium.
- 7a. fused tuberosities of ischium.
- 8.8'. sacra.

Between 4' and 4 is the opening of a double vagina, and in front of it the opening of a urethra.

Between 2 and 2' is the opening of the other (incompletely double) vagina, just external to which is seen the opening of the second urethra.

Fig. 5. Composite femur seen from behind.

- Art.* articular surface of femur at hip-joint.
- Gt. Tr.* great trochanter on one side.
- Gl. R.* gluteal ridge on one side.
- La. La.* linea aspera on one side.
- Add. M.* insertion of adductor magnus.
- Ext. C.* external condyle on one side of lower end of composite femur.
- I. Gr.* inter-condylar groove on one side.

Fig. 6. Front view of the tibia and fibulæ in the composite limb.

Art. on head of fibula of one side, placed just above superior tibio-fibular articulation.

T. subcutaneous part of composite tibia.

L. Pat. insertion of ligamentum patellæ on one side.

T. Gr. insertion of tendon of fused graciles and sartorii muscles.

Fig. 7. Principal nerves and arteries on back of composite limb.

Gt.Sc.N. great sciatic nerve on one side.

Sc. A. sciatic artery on one side.

Ext.P.N. external popliteal nerve on one side.

Int.P.N. internal popliteal nerve „

F.T.N. fused posterior tibial nerve.

F.A.A. „ „ artery.

D. r. deep branch of artery.

C.P.N. calcaneo-plantar nerve on one side.

Ext. Pl., Ext. Pl. external plantar nerve and artery on either side.

Int. Pl. fused internal plantar nerve and artery.

Fig. 8. Shows relations of kidneys, ureters, bladders, uteri, etc., in the monstrosity.

K. kidneys (right and left) of one twin.

K'. kidneys (right and left) of the other twin.

Ao., Ao'. the two aortæ.

Ur. ureters of one twin.

Ur'. ureters of the other twin.

Au., Au'. the two umbilical arteries.

Uch'. urachus.

Bl. bladder.

Ut. uterus.

R. rectum.

PLATE XIII.

Fig. 9. Pelvic skeleton of the monstrosity seen above and from a little to one side.

S. I. fused ischial tuberosities.

I. sp. ischial spine.

S.p. symphysis pubis (compressed).

Obt. F. obturator foramen.

† origin of obturator internus muscle.

Fig. 10. Skeleton of foot of composite limb, showing the composite astragalus, scaphoid, internal cuneiform and first metatarsal (see p. 269).

Fig. 11. Transverse section (diagrammatic) of upper part of thigh of composite limb, to show the double set of muscles and their relations. The composite femur lies in the centre.





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A RARE ANOMALY OF THE AORTIC ARCH. By R. STANLEY TAYLOR, Downing College, and J. M. P. GRELL, Selwyn College, Cambridge.

IN a male subject dissected by us during the Michaelmas term 1901, we found a remarkable series of branches arising from the aortic arch, which we think worthy of putting on record.

The innominate artery was normal in position, but, before its division, gave off a small thyroidea ima and a minute thymic branch. The left carotid was also normal. Between it and the



left subclavian the inferior thyroid artery of the left side arose independently from the aortic arch, close to the root of the subclavian, but separate from it. Its plane of origin was slightly behind that of the contiguous large branches.

From a bulbous enlargement, 8 mm. in diameter, situated in front and at the root of the left subclavian, a large trunk arose, which ascended in front of the left subclavian as far as the medial margin of the scalenus anticus muscle; here it gave off (1) the internal mammary, which descended in its normal position into

RE ANOMALY OF THE AORTIC ARCH.

rtly after this there arose (2) the (3) posterior scapular, and (4) su all crossed over the scalenus antici overal destinations in the usual fast an the left vertebral arose at its the ascending cervical. The vei e quite normal in their relations. io record of any case exactly like prior thyroid from the aorta on the colai (*de Directione Vasorum Diss.* specimen, in which a thyroid vei l with a normal artery arising fro bed by Hyrtl (*Oesterreich. Zeitschrij* 1880, p. 324). Quain figures and the internal mammary, transversa eries, piercing the scalenus anticus, ian trunk, not from the aorta (pl. riations described and figured by H l. viii. (1777), p. 92, is one in whic thyroid and internal mammary aro ian by a common trunk; but no ially are exactly like the case now r feature of interest in this subject w consisted of 7 cervical, 11 thoraci ccygeal vertebræ.

ANOMALIES IN THE CERVICAL AND UPPER THORACIC REGION, INVOLVING THE CERVICAL VERTEBRÆ, FIRST RIB, AND BRACHIAL PLEXUS. By LAWRENCE DUKES, B.A., and S. A. OWEN, B.A., Trinity College, Cambridge.

AN interesting specimen which we have found in the dissecting-room of Cambridge University presents the following series of abnormalities in the cervical and thoracic regions.

The numbers of the vertebræ in the lumbar and thoracic regions respectively are normal. In the cervical region, however, the axis and the 3rd cervical vertebra are extensively synostosed, the synostosis involving the bodies, laminæ, and spines. The bodies of the 2nd and 3rd cervical vertebræ are completely fused, as also are the laminæ and spines on the right side. The costo-transverse processes of the vertebræ are not involved in the fusion, the synostosis commencing immediately behind the articular processes, and the nerves issue normally.

The upper part of the fused spines is especially prominent, whereas the lower part, corresponding with the 3rd cervical vertebra, is blunt and flattened laterally.

The costal element of the costo-transverse process of the atlas is ligamentous on the right side, the vertebral artery passing as normally through a foramen which in this case, however, is partly of a ligamentous and partly of an osseous nature.

The 1st rib consists of three parts—osseous proximal and distal extremities, and an intervening ligamentous portion. The bony proximal extremity includes the head, neck, tubercle, and a very small part of the shaft. This ends ventrally in the ligamentous portion, which presents a somewhat round, cord-like appearance, and is about 3 cms. in length. The ligamentous portion at its proximal extremity is rather narrower and more pointed than at its distal extremity, and takes origin about half a cm. from the tubercle.

The head of the rib presents no remarkable feature. The neck, however, has two grooves impressed upon it. The inner

of these two grooves lodges the vertebral artery, which turns over it to gain the costo-transverse foramen of the 7th cervical vertebra, through which it passes. The outer groove, separated from the former by a well marked ridge, is occupied by the 8th cervical nerve as it passes to take part in the formation of the brachial plexus. This same nerve passes over the ligamentous portion of the 1st rib.

The greater part of the 2nd thoracic nerve enters the brachial plexus by joining the 1st thoracic nerve about 2.5 cm. external to the latter's exit from the inter-vertebral foramen.

To effect this junction it has to pass over the 2nd rib, joining the 1st thoracic nerve at the inner side of the ligamentous portion of the 1st rib. The combined trunk then proceeds outwards over the ligamentous portion of the 1st rib, closely applied to and below the trunk of the 8th cervical nerve.

The remainder of the 2nd thoracic nerve is small. It divides into two branches, which supply the 2nd intercostal space.

The subclavian artery passes over the ligamentous portion of the 1st rib, ventral to the combined trunk of the 1st and 2nd thoracic nerves, and, as usual, behind the scalenus anticus, which is attached to the distal bony portion of the 1st rib, just in front of the termination of the ligamentous portion. The scalenus medius, however, is attached to the 2nd rib.

The "profunda cervicis" branch of the superior intercostal passes backwards between the necks of the 1st and 2nd ribs to reach the muscles of the back.

A CONTRIBUTION TO OUR KNOWLEDGE OF THE
CHEMISTRY OF RED BONE MARROW. By ROBERT
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London Hospital*, and J. J. R. MACLEOD, M.B., *Demonstrator
in Physiology, London Hospital Medical College.*

OUR knowledge of the chemical composition of the red marrow of bone is at present very imperfect, and even in the best text-books of physiological chemistry the subject is dismissed in a few lines. An attempt to extend our knowledge has been occupying the attention of the writers now for some months, but has met with great difficulties. The first obstacle to be overcome was the trouble of obtaining a sufficient supply of fresh material. By using horses' ribs from which the marrow was expressed by a special crushing-machine this difficulty was partially surmounted, but the large proportion of fat present in the product rendered the subsequent chemical manipulations exceedingly troublesome. We have thought it well, however, to embody such results as we have been able to obtain in the present short and admittedly fragmentary paper,—chiefly in order that they may serve as a basis for future research.

General Percentage Composition of Red Marrow.

The following table represents approximately the percentage amounts of the chief constituents of the marrow, as determined by ordinary chemical methods:—

Water	67·42
Solids	32·58
Proteids	11·6
Fat	}	17·9
Lecithin		
Cholesterin		
Soluble Salts	. .	2·34 (of which 0·48 = P_2O_5)
Insoluble „	. .	0·66

Nature of the Proteids.

1. *Method.*—The expressed marrow was macerated in half-per-cent. ammonia solution for twenty-four hours, with the addition of a little thymol. The extract was filtered, and on the addition of dilute acetic acid yielded a large precipitate. Several extractions were thus made, and the united acetic acid precipitates collected, redissolved in dilute ammonia, and reprecipitated at least three times, in order to get rid of fat.

The purified precipitate thus obtained, and now greatly reduced in bulk, was divided into two parts, which were treated as follows:—

1. One part was digested with hydrochloric acid and pepsin for several hours. A dark brown fluid and a brown sediment resulted. The fluid gave peptone and albumose reactions. The sediment was dissolved in weak ammonia, and precipitated by acetic acid. The precipitate gave, after purification, all the reactions of nuclein, the proportion of phosphorus being 0·79 per cent. (one determination).

2. The other part was repeatedly shaken up with 0·8 per cent. HCl in a separating funnel¹ for some hours and filtered. On neutralisation with ammonia, the filtrate yielded a precipitate, which was washed with weak ammonia and redissolved in 0·8 per cent. HCl. The resulting solution gave the following reactions:—

- (a) A precipitate on neutralisation with ammonia.
- (b) No coagulation on boiling.
- (c) A precipitate with nitric acid, which almost entirely disappeared on heating, and returned on cooling.
- (d) A brown precipitate on the addition of iodine in iodide of potash solution.
- (e) No reducing substance on hydrolysis.
- (f) A very slight or no reaction with Millon's reagent.
- (g) A dark violet colour with sulphate of copper and caustic potash.
- (h) A precipitate on saturation with common salt or on half-saturation with sulphate of ammonium.

¹ *Bang. Ztschr f. physiol. Chemie*, Bd. xxx. p. 157.

(i) No precipitate on dialysis.

(j) Ferrocyanide of potash gave a blue solution (? iron) and a slight precipitate; sulpho-cyanide of ammonium, a blood-red colour.

The dialysed solution gave only a very slight haze on boiling; nitric acid yielded a precipitate, which disappeared on heating, and reappeared on cooling; ammonia gave no precipitate till a crystal of common salt was added.

A pure neutral filtered solution of egg albumin gave a copious precipitate, which dissolved on the addition of one drop of 20 per cent. acetic acid, and reappeared on neutralisation with caustic potash.

No iron reactions were obtained with ferrocyanide of potash or ammonium sulpho-cyanide after dialysis.

The result of these experiments seems to show that bone marrow contains (1) a nucleo-proteid, (2) a histon. The presence of the former of these has already been demonstrated by Forrest,¹ and confirmed by Halliburton,² who further points out the peculiar richness of the nuclein of marrow nucleo-proteid in phosphorus (1.6 per cent.).

As regards the histon, it must be confessed that we have had difficulty in satisfying ourselves of its presence in *every* sample of marrow we examined, at all events after dialysis.

The association of disease of the bone marrow with Bence Jones' albumosuria induced us to examine the fresh marrow for that form of albumose. We used both the alcohol and ammonium sulphate methods described in detail in a case of myelopathic albumosuria shortly to be published by Dr Parkes Weber, but in each case with entirely negative results.

Total Alloxuric Bodies in Marrow.

Method.—40 gms. of fresh marrow bone were boiled for three hours with water, the mixture containing $\frac{1}{2}$ per cent. sulphuric acid, and filtered. To the filtrate, neutral and basic lead acetate were then added till no further precipitate appeared. The product was filtered and excess of lead removed by sulphuretted

¹ *Jour. of Physiology*, 1894, xvii. p. 174.

² *Ibid.*, 1895, xviii. p. 306.

hydrogen. The precipitate of PbS was filtered off, and aliquot parts of the filtrate, from which the H_2S was expelled by heat, were treated with ammonia and ammoniacal nitrate of silver. The resulting precipitates were collected and the alloxur bases calculated from the nitrogen which they contained.

Results:

(1st sample) 100 grms. fresh marrow contained 0.1525 grms. alloxur basic-nitrogen = 0.4063 gm. alloxur bases.

(2nd sample) 100 grms. contained 0.1468 gm. alloxur basic-nitrogen = 0.3897 gm. alloxur bases.

We were unable to obtain a sufficiency of material to enable us to investigate the precise nature of the bases present, or the proportion of free to combined bases.¹

The injection of a saline extract of red marrow into the vein of a cat in order to determine its effect on the blood pressure yielded an entirely negative result. Observations on the therapeutic value of the proteids of bone marrow when administered by the mouth to patients suffering from pernicious anæmia were equally inconclusive.

¹ In another experiment we employed baryta in place of the lead salt to separate the sulphuric acid, as this has been shown by Burian and Schur (*Arch. f. d. ges. Physiologie*, Bd. lxxx. S. 241) to yield more accurate results. We found the method inapplicable, however, in the case of bone marrow, on account of the large amount of fat present in the solution.

TWELFTH REPORT ON RECENT TERATOLOGICAL LITERATURE. By BERTRAM C. A. WINDLE, M.D., Sc.D., F.R.S.,
Professor of Anatomy in the University of Birmingham.

[The author of this Report will feel greatly obliged if writers on teratological subjects will supply him with reprints of their papers for use in the preparation of further reports.]

I. EXPERIMENTAL.

FÉRÉ and LUTIER (i.) describe further the experiments which they have made in *grafting embryos* beneath the skin of living fowls and allowing them to grow there. These have been detailed in previous reports in *this Journal*. They now inform us that the earlier the embryo, or part of an embryo, used for grafting, the less rapid are the regressive changes which take place after that operation. Thus, an adult kidney, grafted under the skin or in the peritoneum, becomes absorbed more rapidly than an embryonic kidney in either of the same positions. A large number of instances are recorded in the paper, with an account of the microscopic examination of the objects found. The following may be cited as examples of the experiments. One cock had 172 grafts made in his tissues during the course of a number of years, of which 36 produced tumours. This was rather a large proportion of successes. In another case, out of 107 grafts, 9 produced tumours. In these tumours the greater number of tissues found representatives. In the case of the graft of embryos, a considerable number of the elements survived the operation and persisted in the tumour, presenting there the principal phenomena of growth—hypertrophy, hyperplasia, differentiation. The elements which attain the adult condition persist long enough to lead to the belief that they would live as long as their host. These tumours represent as closely as possible the spontaneous teratomata. An interesting point is, that in old tumours striated muscular fibres are not met with, though they are in tumours removed after a few weeks' development. FÉRÉ and PERTIT (ii.) have a paper further dealing with the structure of these *experimentally produced teratomata*. They point out that many undergo a fibro-cystic change, but the rest are interesting because their minute structure, which is exhaustively described in the paper, proves that they have points in common with the spontaneous teratomata and with the neoplasms of the body. Many of the karyokinetic figures observed were abnormal, and giant cells, containing three or four nuclei, were also found. FÉRÉ (iii.), pursuing his course of experiments in the injection of various substances into the egg prior to incubation, has tried the effect of *antipyrine*. In small doses this

seems to slightly accelerate the pace of development. In larger doses the results are harmful, though no mention is made of the actual occurrence of monstrosities.

II. GENERAL.

RABAUD (iv.), in a paper on the *biological significance of monstrosities*, claims that teratology is not now looked upon quite so much as an appanage of embryology as it used to be. The fact is that teratology and embryology are parallel subjects, both studying the manifestations of organic evolution, but teratology is the wider of the two, for it deals with the ontogenetic variations of the organism. In fact, it is the study of the variations of embryonic evolution which lead to the production of adult forms differing from the normal type, which forms are produced under the influence of nutritive modifications, from whatever cause these may have arisen. Teratology is thus an important branch of biology. MINOT (v.), in a paper on the *embryological basis of heredity*, finds it difficult to believe the hypothesis that a teratoma (or embryoma) arises by the parthenogenetic development of an ovum retained in the parent body. He is also doubtful as to the validity of Bonnet's hypothesis, though he prefers it, viz., that one of the early segmentation spheres gets isolated and retarded in its development, remaining as an inclusion in the foetal tissues, and afterwards developing and producing a variety of tissues *in loco*. He classifies teratological formations under three heads: (1) those which are due to a necrosis of tissues, which apparently rarely, if ever, takes place uniformly throughout the embryo; (2) those due to gross mechanical disturbances of the development, consequent upon failure of the proper correlation of the growth of parts; monsters of this division are probably the most common; (3) those due to errors in the differentiation of tissues or pathological histogenesis. RABAUD (vi.) deals with the doctrine of *arrest and excess of development*, and states his opinion that it does not by any means bear the wide extension which has been assigned to it. He considers the history of the theory, which, he believes, originated with Harvey in 1662, and traces its influence on the work of the two St Hilaires and of Dareste. A true arrest of development, in the strict sense of the term, is difficult to point to; a single kidney may be cited as an example. Many so-called arrests are hypoplasia, e.g., ectromelia. Brachydactyly is an arrest of growth, and of this category dwarfs are complete examples. Again, there is such a thing as arrest of differentiation, though this is rare; an example may be found in the anidei, i.e., aræ vasculosæ, without any contained embryo. Then there are cases in which an embryonic condition, having attained its maximum, ought to pursue a process of regression, but does not. On the contrary, the embryonic condition is maintained, and goes on increasing in size, e.g., uterus duplex. Such cases are really instances of hyperplasia. In spina bifida there is no lack of growth nor of differentiation, but instead of these taking place

in a narrow band of ectoderm, and the proliferation leading to the production of a gutter and then a tube, the neuroblasts have sprung up in a larger area and formed an extensive sheet. Thus there is a diffused differentiation, activity having extended itself to an unusual area. Cyclopia is not an arrest. The brain of the cyclops possesses all the necessary substance to form the anterior cerebral vesicle; there has been no obstacle to the growth or progress of its tissues. Here, again, the ectoderm has been transformed into an unusually large area of nervous tissue; what ought to have been a vesicle has become a large sheet, with a very limited amount of invagination, from which sheet spring one or two eyes. These direct themselves towards the ventral aspect of the embryo; that is to say, they come to occupy an unusual position by a new disposition of the tissue from which they originate, without the intervention of compression or of any mysterious attraction. These forms, and also the Plagioccephali, in which there is a distortion of the cerebro-spinal axis, may be classed as heterotopic differentiations.

A paper by KOLLMANN (vii.) on the circulation in the placenta contains a note on *Telegony* which may, perhaps, be inserted in this report. The conclusions of his paper are as follow: On the surface of the chorionic villi can be seen fine membranes, which are very similar to endothelial membranes. These spring from fragments of the epithelial covering of the chorionic villi. They can be detached from the chorionic villi of the fully developed placenta in men and apes, either by decomposition or by maceration in 30 per cent. alcohol. They are often designated as endothelial membranes. The chorionic villi are directly in contact with the maternal blood; their epithelium is covered by no endothelial membrane. In the first months the chorionic epithelium is possessed of a great productive power. Lateral buds of different kinds spring from the covering layer, which in turn derives its material from Langhans' layer. These lateral buds produce giant cells, knobs, club-shaped processes, bands, so-called canalised fibrin. All these processes consist of nuclear and internuclear protoplasm. The chorionic epithelium arises from the primitive ectoderm, and may be therefore called ectodermal plasmodium, or syncytium, or embryonic plasmodium. In the last analysis its cells spring from segmentation spheres, and therefore contain germ-plasm. Some of the giant cells and other parts of the ectodermal syncytium of the foetus may be carried away by the maternal blood, and such parts, containing germ-plasm, may afford an explanation of the phenomena of *Telegony*.

REGNAULT (viii.), dealing with the subject of *achondroplasia*, as met with in dogs, points out that basset and turnspit varieties occur in all varieties of dogs, and have in some cases been perpetuated by breeding, as in the instance of the dachshund. An examination of the skeleton of these breeds proves the conformity of the condition met with in *achondroplasia* in man especially. (1) The long bones of the limbs are all deformed in the same way as in achondroplastic human skeletons. (2) The muscular ridges and depressions are all very much accentuated, e.g., the deltoid tubercle and the deep hollow for the *tibialis anticus*. (3) The long bones are short and thick. (4) The proportion of the

lengths of the segments is very different from that of other dogs. (5) The pelvis is deformed, the vertical diameter being less than the transverse, which is contrary to the general rule. (6) The skull is normal, as may be the case in achondroplastic men; thus the skull of the basset is that of a normal sized dog. Allusion is also made to basset pigs and to the ancon sheep. The SAME WRITER (ix.), in exhibiting a case of *achondroplasia* in the human species, points out that there are two varieties, hyperplastic and hypoplastic. In any given case it is necessary to examine whether (1) the curves are accentuated, and (2) the extent of the thickening of the bones, for these two lesions are not always in direct relation to one another. Kaufmann, says the author (*Untersuch. ub. d. sog. foet. rachitis*, Berlin, 1892), describes a third variety, which he calls chondromalacia. In this form the malady is accompanied by a softening of the cartilages. In this case the thickened bones, arrested also in length, are profoundly softened, and present the appearances of an extreme degree of osteomalacia. A further paper on *chondrodystrophia foetalis* is contributed by COLLMAN (x.), and a note to the same is made by Virchow.

FELDMAIER (xi.) narrates a case of *hermaphroditism* in which the external genitalia were those of a female, a hymen being present, and the individual was brought up as belonging to that sex. The testicles descending later caused trouble, and their removal led to the discovery of the real nature of the case. In addition to the theory mentioned under vi., the following conclusions on the subject of *spina bifida*, from another paper by RABAUD (xii.), may be quoted: *Spina bifida* results from an interesting modification of the medullary portion of the nervous system. The spinal fissure, properly so called, is a result of this initial process. Camille Dareste (1877), Tourneux and Martin (1881), have previously arrived at this conclusion from embryological data. Two types of *spina bifida* must be distinguished. The first, which is compatible with existence, is characterised by the existence of a more or less voluminous pouch. The second, a very grave anomaly, accompanies anencephaly. It is characterised by a complete amyle and by a spinal fissure open to the air. The first type, the only one which interests the surgeon, includes internal hydrorachis or myelocystocele and external hydrorachis or myelo-meningocele. In both cases the cord is entirely closed by a proper neuro-epithelial covering which is completely nervous. This closure takes place late in the course of embryonic development by the confluence of the lateral ectodermic folds, a process comparable to the formation of the amnion. The amount of nervous elements entering into the composition of the dorsal covering is very variable. This dorsal covering is overlaid by a greater or lesser amount of connective tissue under various forms and by the skin. It follows from this that the cavity of the pouch of the *spina bifida* is only an objective dilatation of the ependymal canal. This cavity is in direct continuity with the canal forwards and backwards, so that it is not, as Tourneux and Martin affirm, a dependance of the subarachnoid spaces. Pathological processes may intervene and modify the aspect of the *spina bifida*. The nervous tissue in particular

may be overtaken by degeneration. The pouch is then more or less open, and communicates with the submeningeal spaces. From this there results a large cavity traversed by nervous tracts. The efficient cause of spina bifida is neither mechanical nor pathological, but is to be found in the actions and reactions of the tissues and their environment. GUIRYESSE and RABAUD (xiii.) describe a foetus affected with *ectropium of the bladder*, spina bifida, talipes, and other defects. Some of these they attribute to mechanical causes. Thus the two glutei muscles of opposite sides are fused into a single large muscle, a condition which they think is due to the absence of the vertebral laminae of the sacral region, the consequence of the spina bifida. There was no union of the two sides of the pelvis at the symphysis pubis, and the contraction of the glutei muscles had pulled the two halves apart so as to cause a symmetrical deformity of the pelvis and an abnormal position of the two lower limbs.

III. DUPLICITY.

KAESTNER (xiv.), in his third paper on *double monstrosities* of the embryonic area in birds, describes the microscopic examination of several cases. He points out that transverse sections through the two primitive grooves lying close to one another show that the space between the two is occupied by dense mesoderm, so that there is no line of separation between the two anlagen. He also shows, from a specimen which has come under his notice, that two primitive streaks on one germinal area do not always lead to the production of a double monstrosity, but that one of them may be arrested at a very early stage of its development, so that the other is in a position to proceed to a normal process of development.

GEMMILL (xv.) has contributed a very valuable paper, at present available only in abstract, on *double malformations in the trout*. In this paper it is shown that at the region of transition in laterally symmetrical double monstrosities the notochords are the last structures to unite, while equally primitive structures, both dorsal and ventral to the notochords, viz., the neural axis and the alimentary canal, lose their duplicity earlier. It is further shown that those parts of the neural axis and alimentary canal which are most closely apposed to the notochords retain evidence of original duplicity longer than parts which are more remote. The floor and roof of the neural axis and of the alimentary canal are to be seen in marked contrast in this respect. Duplicity of the dorsal aorta, of the pronephric glomerulus, of the vertebral cartilages, of the body muscles, and of various other structures, is correlated with duplicity of the notochord. In paired organs the transition from the double to the single condition takes place at the expense of the inner or adjacent elements, which are usually united and reduced in size before they disappear altogether. From the evidence brought forward it is inferred that fusion has played a not unimportant part in moulding the form of the neural axis and the

alimentary tract in the transition region. The union of adjacent paired structures is probably to be explained by the fusion of mesoblastic blastema developing laterally from each of the embryonic axes near the place of convergence and union. The law that union takes place between homologous structures always holds good. Both twins usually contribute equally and symmetrically to the sum of structures in the transitional region. Another valuable paper on an almost identical subject is that of SCHMITT (xvi.) on *double embryos amongst the salmonidæ*. The forms which he has observed are divided by the author into seven groups, viz., (A) Embryos united only indirectly by the yolk sac. (B) Union purely ventral. (C) Union approximately ventral. (D) Union half ventral, half lateral. (E) Union approximately lateral. (F) Union purely lateral. (G) Double embryos externally appearing to be single. It will be observed that the author excludes from his classification parasitic forms, which have found a place in the arrangements proposed by Lereboullet and by the present reporter. The paper contains a very elaborate account of a number of embryos, microscopically examined, but of a character impossible to be summarised. SOBOTTA (xvii.) sums up much of what has recently been written on the subject of homologous twins amongst human beings, and states it as his opinion that their origin must not be assigned to the separation of the two first segmentation spheres of the ovum. LESBRE (xviii.) describes the anatomy of a *deradelphous lamb*. The condition is one of duplicity posterior to the umbilicus, a single head with three or four thoracic members. It is common amongst mammals, especially the cat, but rare in man. A case has been met with where it occurred in a pair of grey lizards. In the case under description the usual torsion had carried two of the thoracic limbs on to the dorsal aspect of the body. The anatomy, which is carefully described, does not materially differ from that of other specimens of the same class which have previously been recorded. CROUZAT (xix.) gives an account of a living pair of *xiphopagous twins*. In view of the probable relation of at least some forms of teratomata with duplicity, and the connection of the former with dermoid tumours of the ovary, some notes of papers on these subjects are here appended. LEXER (xx.) describes (1) simple and complicated *dermoids*, (2) foetal inclusions, and (3) mixed teratoid tumours of the abdomen, and deals especially with their situation. Simple dermoids occupy different positions according to the place of their origin: (a) those cut off in the omentum and mesentery by the closure of the abdominal wall. He thinks that dermoids lying between the layers of the mesentery have the same origin, though (b) those retroperitoneal dermoids which belong to the lumbar region, he thinks, have originated from the Wolffian body. (c) The rare dermoids growing from the retrorectal tissues may extend as high as the umbilicus; (d) multiple dermoids of the abdominal cavity may be traced back to transplantation from an ovarian dermoid which has fissured. Complicated dermoids are, for the most part, detached ovarian tissue, and lie mostly in the lower part of the abdomen, and in connection with the omentum and with the mesentery. They may, however, wander as far as the transverse colon; one

of the author's cases was found in the ileo-cæcal region. In another instance a large complicated dermoid of the lower part of the abdomen was connected with a retained testis. (2) The undoubted foetal inclusions are found most commonly in the transverse mesocolon, or in connection with the lesser sac of the omentum. The latter situation is explained by the fact that any parasitic germ implanted in the coelom of the upper part of the abdomen, if between stomach and liver, must be drawn into the lesser sac by the shift in position of the first-named organ.

(3) Of the seven cases heretofore described of teratoid tumours of the abdominal cavity gathered together by the author, five are certainly to be regarded as bigerminal implantations. He adds to these a case of his own where the tumour was removed by operation from a girl of 11 years. This tumour lay in the lesser sac of the omentum; its firmest place of attachment was to the pancreas, which was dragged upwards. The tumour consisted of two parts, a sac and a solid kidney-shaped mass. The latter consisted chiefly of adipose tissue, but enclosed small cysts, mostly lined with mucous membrane, and in one case dermoids. There were also knobs of cartilage, a piece of bone with contained marrow. There were representatives of all three primitive layers. BANDLER (xxi.) has a paper of great length and complexity, which extends over several numbers of the *American Journal of Obstetrics*, and is illustrated by a large number of figures, dealing with the subjects of *dermoid and other cysts of the ovary*. He believes that these tumours originate from the Wolffian body. SCHOU (xxii.) describes a *dermoid tumour* of the ovary removed from a child æt. 7. It contained four teeth, a rudimentary alveolar process, and balls of hair.

BACKHAUS (xxiii.) describes a *dermoid* which was removed by operation from a girl of 17. It was steatomatous in its character, and within it were found a tooth, skin, hair, cerebral material, bone, and unstriped muscular tissue. It was malignant in its character, and the patient eventually succumbed to secondary growths derived from it.

IV. HEAD AND NECK.

KOTSCHETKOWA (xxiv.), in an inaugural dissertation, deals with the subjects of *microgyry* and *microcephaly*. The first case described, which was that of a female aged 20, was one of highly developed microgyry of the right cerebral hemisphere, with hemiatrophy and microgyry of the opposite cerebellar hemisphere. In the most profoundly altered convolutions there was present extreme proliferation of the neuroglia, which had stretched as a diffuse sclerosis far over the limits of the primary focus, and had caused a considerable decrease of the nervous elements and a shrinkage of the convolutions, the lesion affecting the medullary as well as the cortical portions. The second case was that of a child aged 7½. The microscopic condition of the brain in both cases is fully described at considerable length.

LEHMAN-NITSCHKE (xxv.) figures and describes a remarkable mal-

formation of the face. The nose was divided into two portions, each consisting of a single nostril, which two portions were separated from one another by a considerable interval. The person affected was a male, aged 18. GIUFFRIDA-RUGGIERI (xxvi.) has a paper on *bipartite nasal bones*, and on Wormian bones of the post-frontal region and of other parts of the facial skeleton. SCHWALBE (xxvii.) has a paper on *abnormal fissures and bones of the skull*. (1) Frontal suture, regularly present in all mammals. It is of rarer occurrence amongst adult apes than in man. The author has never seen it in an adult anthropoid ape. (2) The varying patterns of pterion are compared with those met with in apes. (3) Ossa bregmatica are to be looked upon as individual variations, fontanelle bones. (4) Os parietale bipartitum, rare in man, and once found in an orang. An incomplete fissure has been found once in chimpanzee, once in young gorilla, in a cynocephalus and in a mycetes, but not in hylobates. (5) The interparietal bone is also dealt with.

REGNAULT (xxviii.) describes a case of *partial fusion between the occiput and atlas* which he believes to have been due to congenital rather than to post-natal disease, because the union of the two parts of the posterior arch has been interrupted; the atlas is thin and atrophic. The union of the right half of the posterior arch with the skull is very firm, the two bones seeming to form one. The condition recalls that of the precocious union of cranial sutures. APERT (xxix.) describes *another specimen of the same kind*. The anterior arch is almost entirely united with the occiput, the posterior arch is separated from it, and its two halves are ununited. This last peculiarity is a feature of other skulls presenting the same condition, and seems to show that the pathological process causing the defect is one which takes place before the union of the two halves of the posterior arch. JEANBRAN (xxx.) records a *congenital cyst of the neck*, situated in the upper left carotid region. It was in part adherent to the internal jugular vein and contained gelatinous matter. Its wall consisted of stratified epithelium, connective tissue, with round cells and lymphoid follicles. WEILL and PÉHU (xxxi.) describe a case of *congenital defect of the œsophagus*, in which there was a considerable interval between the upper and lower segments, the latter communicating freely with the trachea. SHATTOCK (xxxii.) has some observations on an *imperforate pharynx* which existed in an agnathic lamb. The former condition is one of the rarest of defects, and never met with except as an accompaniment to synotia, cyclocephalus, or nanocephalus; a curious fact, seeing how common imperforate anus is. The condition must be carefully distinguished from that of atresia of the œsophagus, a common enough defect, since the two malformations have no connection with one another. Atresia of the œsophagus is invariably situated opposite the lower end of the trachea, and is a condition acquired in fetal life, and probably in some way connected with the voluminous growth of the lungs and lower part of the trachea as a diverticulum from this spot of the anterior wall of the œsophagus. In imperforate pharynx the disposition corresponds with what would arise from the abnormal persistence of a normal phase of development.

His's researches have shown that the stomodæum produces hardly any of the buccal cavity ; that the entire tongue is formed from the floor of the blind pharynx ; all these points were illustrated in the specimen exhibited, in which the lower jaw was wanting ; the stomodæum was represented in part by an area of mucous membrane covering the under side of the exposed palate, and in part by the nasal cavity. There was no communication, however, between these parts and the post-jacent pharynx, from the floor of which a well developed tongue projected. V. HIPPEL (xxxiii.) describes a case of *partial absence of the iris* with hæmophthalmus, and points out that what clinically appears to be a condition of complete absence of the iris is not really such, but one of extreme retraction of that part of the eye. MARFAN and DE LILLE (xxxiv.) record certain malformations in a child aged 3½ months, which had suffered from *facial paralysis* from birth. The paralysis affected the right side, and it was noticed that there was a malformation of the external ear of the same side. The external auditory canal was rudimentary, and there appeared to be no tympanic cavity. After death it was discovered that the child had no right internal ear. The brain was normal, but the nuclei of the right facial nerve were in an atrophic condition. BYWATER (xxxv.) describes a case of *bifid tongue* in a man, the cleft extending for a quarter of an inch into the organ.

V. THORAX.

VALENTI (xxxvi.) found in a subject that the *third rib*, which was normal as far as its tubercle, then became wider and *bifurcated* at its anterior angle. It was perforated shortly beyond the posterior limit of the expanded portion. BLONDEL (xxxvii.) narrates an instance of *malformation of the heart*, in which the two ventricles communicated with one another. A pillar of the mitral valve passed across the orifice of communication, and inserted itself in the right ventricle. There was only one auricle, which was situated above the inter-ventricular communication.

VI. ABDOMEN.

DELESTRE and HARET (xxxviii.) note a case of *congenital hydronephrosis* in a stillborn child. BAUER (xxxix.) adds another to the list of *single kidneys*. The missing organ was that of the left side, and the ureter and vesicula seminalis of the same side were also absent. PORAK and DURANTE (xl.) record a case of *diaphragmatic hernia*, as usual occurring at the posterior left aspect of the organ. The left pleural cavity contained the left lobe of the liver, the stomach, spleen, all the small intestines, including the duodenum, the cæcum, ascending and transverse colons, and one-half of the pancreas. *Another similar case*, with the aperture in the same position, is recorded by CONSTANTIN-DANIEL (xli.). CAVALIÉ (xlii.) records what he believes to have been a case of *double ovary*. On the right side the ovary seems to

have been formed of two masses, each of about the same size, which were united by a short, constricted portion. The two portions form two sides of an obtuse angle. Each appears to be the equivalent of a normal ovary. ESSEN-MÖLLER and ENGSTRÖM deal with the *same subject* (xliii.). The former dissected the abdomen and pelvis of a child which had died two days after birth. The uterus was well developed, the right ovary normal, the left small, though not displaced. A second ovary lay attached to the end of the left tube by a short round pedicle. In the instance given by the latter author, the patient was aged 29, and had been three times pregnant. There was a dermoid on the left side, but part of the ovary seemed to be cut off entirely from the growth. LAUBER (xliv.) records a case of *partial persistence of the posterior cardinal vein* in a man. The two cardinals persisted to the level of the kidneys, where there was a cross union. The inferior vena cava came from the right renal vein. The remaining and larger trunk passed upwards, taking the course of the vena azygos major, and emptied itself as that vein. CORDES (xlv.) describes a case of *congenital occlusion of the duodenum*. It occurred in a female infant which survived its birth four days, and the occlusion was just above the opening of the ductus communis choledochus. According to the author, this is the fifty-seventh case of the kind recorded in the literature of the subject. KONIKOW (xlv.) mentions a case in which a *transverse septum* extended across the *vagina* $2\frac{1}{2}$ inches above the vulva.

VII. EXTREMITIES.

EIGENMANN and Cox give a very interesting example of *duplicity in the upper limb* in a frog (xlvii.). The right forearm and hand were double, and the extra member lay on the ventral surface of the normal, and directed obliquely towards the left eye. Another curious feature of the case was that the extra member was bound down to the body, strapped to it by a fold of skin under the throat. SHARP (xlviii.) observed a case of *polydactyly* in which there was a double thumb on each hand. That of the left hand had three phalanges, but the right had only two. The father and one of his sisters had an additional pollex, but none of the rest of the family (nine in number) had this defect. One of the boy's great-uncles was similarly affected. SALOMONSON (xlix.) adds a further case of *supernumerary pollex*, studied by the aid of the Röntgen rays, in a person of 14. There was a single epiphysis for the metacarpal bone, and then again a single, somewhat saddle-shaped epiphysis, with which articulated the two distinct phalanges by which the thumb was terminated. PÉRAIRE (l.) adds a case of *additional minimus* articulating with the unciform, which had an extra facet for it.

JOACHIMSTAL (li.) describes a case of *doubled index*. The right thumb had a small extra phalanx between the ungual and next normal phalanx. Electrical stimuli proved that this method of describing the digits of the left hand was the correct one, otherwise one would have

been inclined to think that the case was one of trimerous ulnar thumb, with normal pollex to the radial side of it, a condition which is known to exist. The SAME AUTHOR (lii.) describes a case of *polydactyly* in a female child aged 3 days. There were six fingers on each hand and six toes on each foot. The fifth and sixth toes were bound together in the same skin sheath. The fingers, which were attached only by skin, were removed. The father was also polydactylous. His left foot had a postminimus, and on the right side the minimus had a bifurcated metatarsal bone. In both feet the ungual phalanx of the great toe was bifurcated partially, and each possessed three sesamoid bones. In the left hand the ungual phalanx was double and the next segment partly so. In the right, both of these phalanges were partly double, and an extra digit had been removed in childhood. Of ten sisters of the child above mentioned, six showed polydactyly. PRITZNER (liii.) has some notes on the following *additional ossicles*: (1) os prætrapezium; (2) sesamoid bone in the posterior aspect of the knee-joint; (3) os trigonum tarsi; (4) sesamoid bone in the interphalangeal joint of the great toe. WEBB (liv.) gives an account of a case of hereditary brachydactyly which ran through seven generations in the female line. In the fingers the second phalanges, and in the thumbs the first, were abnormally short. JEANBRAN and DAUPHIN (lv.) narrate a case of *ectromelia*. On the right side the radius was only the length of the first phalanx of a normal thumb; it was attached to the humerus, the lower end of which was considerably modified, the trochlea being almost double the natural size. The ulna was bent so as to form an arc of a circle with antero-external concavity. The thumb, first metacarpal bone, trapezium, scaphoid, and semi-lunar were absent. On the left side there was no humerus, the forearm articulating directly with the scapula. The ulna was 2 cm. shorter than that of the right side, and was quite straight. It articulated above with a small bone, which may be looked upon either as the much diminished humerus or as the radius. In the hand, the phalanges of the thumb and index finger, the trapezium and trapezoid, scaphoid and lunare, were all absent. The hook of the unciform was hardly marked, but the pisiform was three times the normal size. LONGUET and PÉRAIRE (lvi.) recount an instance of *malformed ulna*. This bone terminated by a pointed extremity, which was united to the radius. There was no power of pronation or supination. The SAME AUTHORS (lvii.) give notes of a case in which the *radius, thumb, and some of the bones of the carpus were absent*, those present being the scaphoid, cuneiform, trapezium, and unciform. The ulna was curved.

GROSSE (lviii.) adds an instance of *absence of the tibia*, and STEINHAUS (lix.) has a paper on *congenital deficiencies of the same bone*.

BREMNER (lx.) notes the coexistence of spina bifida with *congenital dislocation of the hip-joint* in a case which came under his notice.

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ON THE HOMOLOGIES OF THE CEREBRAL SULCI. By
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FOR some time I have been engaged in the task of attempting to determine the meaning and morphological value of the furrows on the surface of the cerebral hemisphere. With this aim in view I have examined the brain in almost every mammalian genus, and have neglected no species which can contribute any material evidence regarding the problem at issue. I have also studied the developmental history of the furrows in some members of almost every Order. The conclusions drawn from these two sources of information have been further confirmed by the data afforded by the examination of moulds of the cranial cavities of extinct mammals, especially those of the Eocene period. For at that time the mammals were still in their infancy, and the pattern formed by the sulci in the progenitors of the various Orders had so slightly diverged from the common pro-mammalian plan that there can be no difficulty concerning the certain recognition of the homologous sulci in the different Orders.

As the result of these converging lines of investigation, I have been able to formulate certain definite views regarding the possibility of homologising the sulci in the brain of one mammal with those of another, which are founded upon such a broad basis of irrefutable facts that their essential truth must, I believe, be ultimately admitted even by those who at present adopt other hypotheses of an utterly contradictory character.

The data culled from the first of the three sources (indicated above) have been stated (with as much detail as—or, as some readers may think, considerably more than—is permissible in a work of such a nature) in the Descriptive Catalogue of the Museum of the Royal College of Surgeons, which is now in the press. The interpretation of the whole body of evidence has been discussed in a memoir on the brain in the Lemurs, which is now being published.

In these notes I shall merely state, without discussing the reasons, the conclusions arrived at concerning the most funda-

mental matters which lie at the root of the whole problem of the interpretation of the furrows on the surface of the cerebral hemisphere. If these can be shown to be erroneous, the whole theory of the homology of sulci which is put forward in the above-quoted works will, *ipso facto*, become utterly futile. I publish these bare results, therefore, so that a definite issue may be raised, and that the criticisms which I hope will be levelled against such heterodox views may be aimed at the essential points, and not at some trivial and relatively unimportant matter arising from the discussion of the homologies of the less stable furrows, concerning which there may be a legitimate difference of opinion.

No fissure or sulcus in the brain of the Mammalia is represented in any form whatsoever in the Reptilia or other Vertebrata.

The hippocampal and rhinal fissures are the only furrows in the hemisphere of the Monotremata which can be homologised with certainty with those of other mammals.

The hippocampal is the only fissure which is present in all mammals; although it may become practically obliterated in certain adult Odontoceti.

The rhinal fissure is almost equally constant, being found in all mammals except the smallest representatives of the Marsupialia (*Notoryctes*), Insectivora (practically all the Centetidæ, Macroscelididæ, in *Chrysochloris* and others), Chiroptera (practically all, the disappearance being secondary in *Pteropus* and *Cynonycteris*), and Edentata (*Chlamydomorphus*). In many mammals this fissure develops in the ordinary manner, and subsequently becomes obliterated. This happens in many Primates and in certain Chiroptera, Rodents, and Ungulates.

These two fissures—hippocampal and rhinal—may be recognised with absolute certainty by the histological features of their lips, as well as for obvious morphological reasons. For they are both limiting furrows of the neopallium, the one separating it from the fascia dentata, the other from the lobus pyriformis.

The development of the hippocampal fissure is not directly, if at all, causally-related to the increasing size of the neopallium. It is due to the peculiar superficial hypertrophy of the marginal

fringe of the hippocampal formation, which leads to the formation of the fascia dentata as an excrescence: this rolls over, so to speak, on the rest of the hippocampus, and the peculiar cleft which we call hippocampal [dentate] fissure is one of the results.

The rhinal fissure is undoubtedly caused by the unequal rates of growth of the pyriform lobe and the neopallium.

Those furrows, which are situated *in* the neopallium, may be called "sulci" in contradistinction to the rhinal and hippocampal "fissures" which separate the neopallium from other pallial areas. It is customary to call certain neopallial furrows such as the Sylvian and calcarine by the name "fissure," whereas others are called "sulci." However useful such a distinction may be in Human Anatomy, its adoption in Comparative Anatomy is undesirable, because it is arbitrary and misleading, and utterly incapable of being accurately applied, for reasons which will become patent in the following notes. It is much more serviceable to use these two terms "sulcus" and "fissure" to distinguish the neopallial furrows from those which bound the neopallium without being placed within it.

Both ontogenetically and phylogenetically the sulci (as just defined) are more recent than the fissures: they are, moreover, not nearly so constant nor so stable as the latter.

Among the sulci are found furrows of varying degrees of stability—some being undoubtedly represented in most Eutheria and Metatheria, whereas others have so little morphological value that they cannot be recognised with certainty in the two cerebral hemispheres of the same brain. Between these two extremes there are sulci of every degree of morphological individuality.

Those sulci which may be regarded as the common property of the Eutheria, and not the exclusive distinction of an Order of mammals, are represented in the accompanying schemata. Their relative degrees of constancy, stability and ontogenetic precocity may be expressed approximately in the following order:—calcarine, suprasylvian, orbital, coronal, lateral, pseudosylvian, diagonal, crucial, postsylvian, intercalary, genual and retrocalcarine. In these notes I shall refer chiefly to the calcarine and the suprasylvian sulci, because their correct inter-

pretation forms the keystone of the whole morphological superstructure which I wish to build up.

The calcarine sulcus is the most widely distributed neopallial furrow (with the possible exception of the orbital). It is present in the Polyprotodont Marsupialia (*Thylacinus* and *Sarcophilus*), in all the Diprotodontia (with the possible occasional exception of *Phascolomys*), in *Galeopithecus*, in the Chiroptera (*Pteropus* and *Cynonycteris*), in the Edentata (excepting only *Chlamydophorus*), in all Carnivora, Ungulata, Cetacea and Primates, and, in most cases, in the Sirenia. Its absence in most Rodents

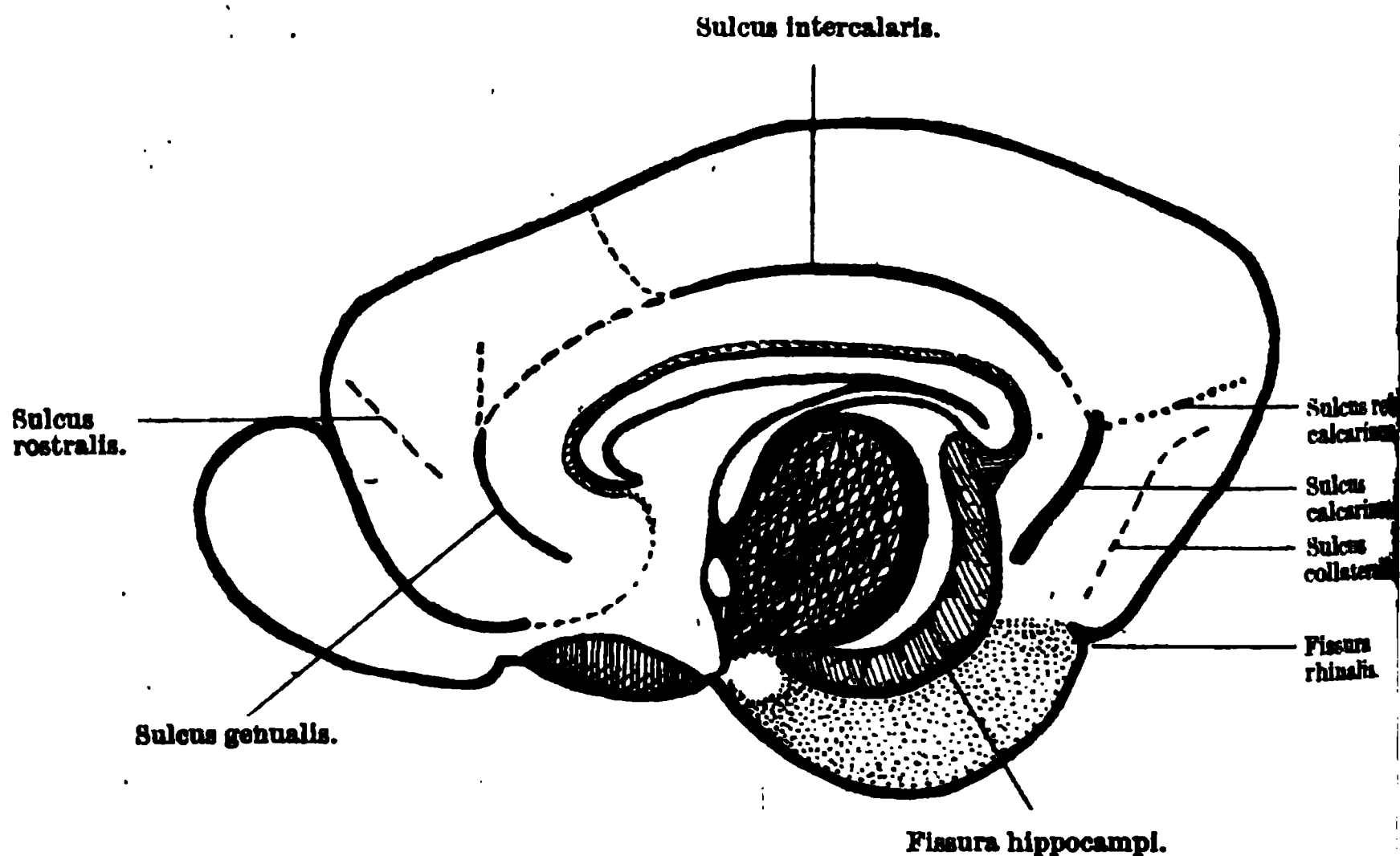


FIG. 1.—Mesial aspect.

is the most peculiar fact so far as its distribution is concerned. Its identity in all these forms is beyond question, for every gradation in the relations of this sulcus, which occur in the Mammalia in general, are also found in the Primates, in which the homology is obvious. A posterior cornu of the lateral ventricle is not a condition necessary for the existence of either the calcar avis or the calcarine sulcus.

In most mammals the calcarine sulcus becomes confluent with the intercalary sulcus. This is a furrow of little morphological importance, which has hitherto received no exclusive title. As it is intercalated between the calcarine, genual and crucial sulci, to

one or all of which it may be joined, I have given it a name indicating this, its most distinctive, feature. The union of the calcarine and intercalary sulci is commonly called "Splenial" (Krueg) in such mammals as Carnivora, Ungulata and Cetacea. When the intercalary and genual sulci are linked, the complex is called calloso-marginal.

The calcarine sulcus remains quite separate from the intercalary in the Primates and the three Edentate families, Myrmecophagidæ, Bradypodidæ and Manidæ. In the former it usually becomes confluent with a morphologically unimportant retrocalcarine sulcus (Cunningham's "posterior calcarine fissure").

All the other furrows on the mesial surface of the brain—collateral, parieto-occipital and rostral—are of little morphological importance and are very unstable. The two former sulci are quite recent in comparison with the relatively ancient calcarine sulcus. They arise in response to special mechanical conditions in the Primates, and are essentially compensatory to the calcarine sulcus. Only slightly less constant than the calcarine sulcus on the mesial surface is the suprasylvian sulcus on the lateral aspect of the hemisphere. It is the "super-sylvian" furrow of Owen, the "suprasylvian" of Krueg, the "anterior suprasylvian" of most recent writers.

The sulcus suprasylvius makes its appearance in the embryo at about the same time as the calcarine, and in almost all cases before the other sulci. It is generally much deeper than any other sulcus on the cranial surface of the hemisphere.

It occurs in Marsupials, in *Galeopithecus*, in several Rodents, (*Hydrochaerus* and *Dolichotis* among others), in Chiroptera (*Pteropus* and *Cynonycteris*), in all Edentates except the smallest Dasypodidæ (*Chamydophorus* and *Tolypeutes*), in all Ungulates, Carnivores, Cetacea and Primates without exception. It is in every respect the most stable sulcus on the lateral aspect of the hemisphere.

In the Carnivora the sulcus is frequently joined to a much less stable and relatively important sulcus, which Owen called "post-sylvian." This is usually distinguished by the misleading title "posterior suprasylvian" (Krueg); Owen's designation is, however, more accurate and less liable to give rise to confusion,

and has the added claim of priority. In some Ungulates the anterior end of the sulcus suprasylvius is linked to the coronal (Krueg); in others, as well as in many Carnivores, it becomes confluent with the diagonal (Krueg)—fig. 2.

In many mammals, such as most Carnivora, the posterior part of the hemisphere is flexed downwards on the anterior part (which is supported and held in position by the basal ganglia): the result of this bending is the development of a suprarhinal

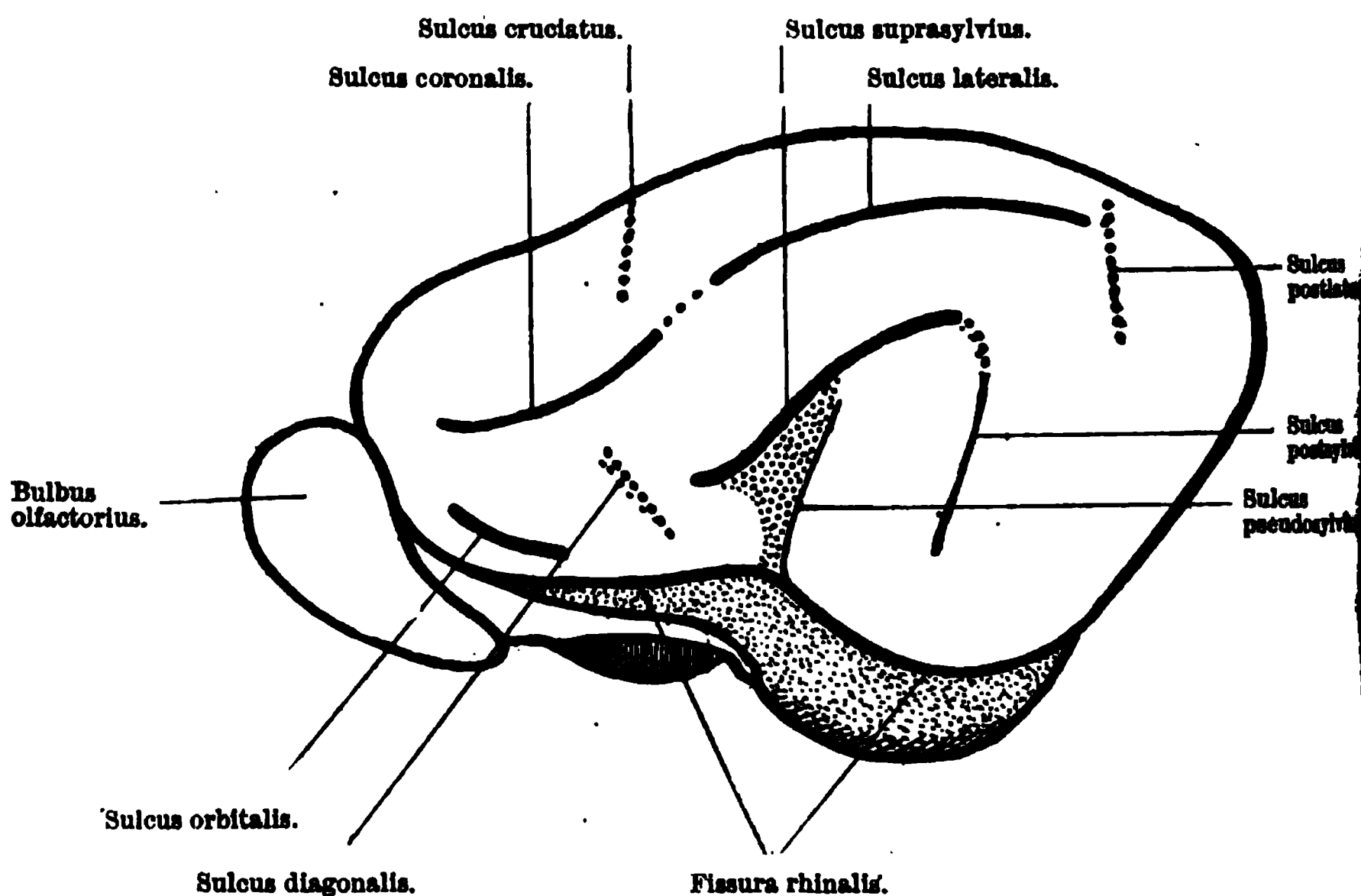


FIG. 2.—Lateral aspect.

kink, which is commonly, though erroneously, termed "Sylvian fissure" by almost every writer. Holl¹ is the only anatomist, so far as I am aware, who recognises the fallacy of this patent error. The simplest form of this false "Sylvian" or pseudosylvian sulcus is seen in the *Æluroid* Carnivora and *Bradypus*.

In most Carnivora the suprasylvian and postsylvian sulci unite to form a great inverted-U-shaped furrow surrounding the pseudosylvian sulcus, from which it is separated by a broad cortical area. The latter is further subdivided (except in the smaller members of the Order, such, for example, as *Ictonyx* and

¹ "Über die Insel," etc., *Archiv für Anat. und Phys.*, Anat. Abth., 1900.

many others) by a very unstable pair of supplementary furrows called ectosylvian—an anterior sulcus between the suprasylvian and pseudosylvian and a posterior between the latter and the postsylvian. [These furrows are not represented in the diagram (fig. 2), because their range in the Mammalia is limited.]

In many Carnivores, *e.g.* *Hyaena*, the anterior ectosylvian sulcus disappears or becomes merged in the pseudosylvian sulcus; in others (all the Arctoidea) the two ectosylvian furrows become submerged in the pseudosylvian cleft and in many of the smaller Arctoid forms become completely obliterated. There is also a pronounced tendency in many Bears and in the Arctoidea generally for the suprasylvian sulcus to approach the pseudosylvian sulcus. In most Seals the cortical area which separates these two furrows becomes submerged so that the suprasylvian sulcus appears to be swept into the pseudosylvian cleft.

In the Edentate *Myrmecophaga* and the Rodent *Dolichotis* the narrow area separating the suprasylvian and pseudosylvian furrows becomes submerged so that the two sulci seem to blend and form one sulcus. A similar phenomenon occurs in all Primates except *Chiromys*, which alone remains to remind us that the "Sylvian fissure" is really a complex of the two sulci—suprasylvian and pseudosylvian (fig. 3).

The Sylvian fissure of the Primates is formed by the posterior opercular lip of the pseudosylvian sulcus extending forward (upward) to meet the anterior (dorsal) opercular lip of the lower part of the suprasylvian sulcus. The peculiar form of the "fissure" is determined by the pseudosylvian sulcus, and its dorso-anterior limit becomes fixed by the stable suprasylvian sulcus. In other words, a kink-like furrow—the unstable pseudosylvian sulcus—is formed by the flexure of the hemisphere. It tends as it deepens to draw into itself an increasing area of neopallium in front of the bend, until it reaches the situation of the deep stable suprasylvian sulcus, which finally limits this process. Thus the suprasylvian sulcus comes to form the dorsal limiting furrow (Marchand's "opercular sulcus") of the island of Reil (fig. 3). After the typical *primate* sylvian furrow is so formed, the submerged area or insula becomes further hedged in by the development of an operculum from the anterior lip of the diagonal sulcus of Krueg (the fronto-orbital

sulcus, the anterior limiting furrow of the insula). This process begins in many specimens of Anthropoid Apes, but only in Man does this anterior (orbital) operculum ever become sufficiently extensive to cover the anterior insular area. The *complete* Sylvian fissure is a distinctive human characteristic.

The orbital sulcus ["presylvian" (Owen), "supraorbital" (Flower), "triradiate" (Turner)] occurs in every Order; but in spite of this wide range it exhibits more variability within any

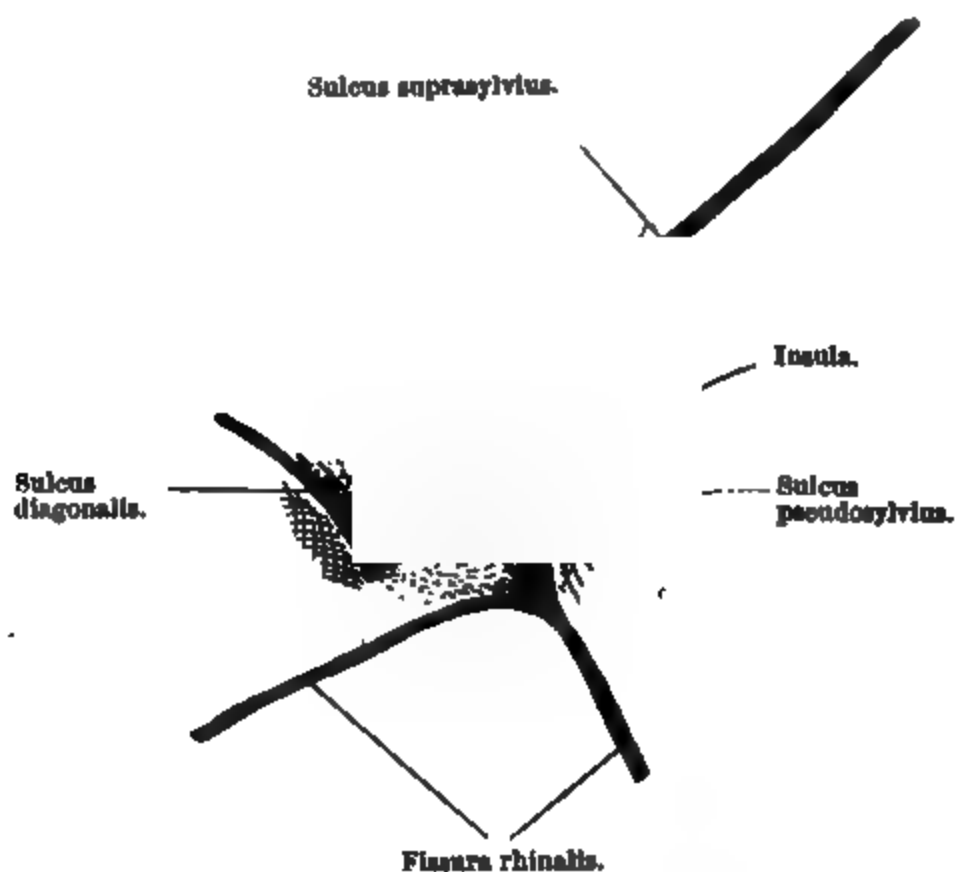


FIG. 3.—A Scheme showing the arrangement of the three elements of the Sylvian fissure.

given Order than either the suprasylvian or calcarine sulcus does. Phylogenetically it is the earliest neopallial furrow, but ontogenetically it is rarely so precocious as the calcarine, suprasylvian, or even the coronal sulcus.

The lateral sulcus occurs in the Diprotodont Marsupials, the Rodents, the Edentates and Carnivores (in both of these Orders it is usually joined to the coronal sulcus), the Ungulata, Chiroptera and Cetacea. In the Primates it is not so stable as the suprasylvian sulcus, for it is absent in *Tarsius*, *Microcebus* and the Hapalidæ. It is more generally known in the Primates as the "intraparietal" of Turner ("interparietal" of German writers).

The lateral sulcus is occasionally found in some mammals, *e.g.* *Tamandua* and *Pteropus*, when the suprasylvian is absent. But there are good reasons for believing that the latter sulcus in these specialised brains has been secondarily obliterated. In most representatives of these two genera the suprasylvian sulcus is present.

The less important and more variable postlateral furrow becomes the sulcus occipitalis transversus.

The postsylvian sulcus becomes the parallel (superior temporal) furrow in the Primates.

The coronal sulcus is even more precocious than the lateral, and in the Ungulata seems to be also more stable. In *Procavia* the lateral is often missing or even absent, whereas the coronal is always well developed. In some small Carnivora, such as *Herpestes* and *Crossarchus*, the coronal sulcus is rudimentary, and may even be absent, whereas the lateral sulcus is well developed.

A study of the Lemurs seems to point to the conclusion that the posterior extremity of the coronal sulcus becomes separated from the rest and linked to the crucial sulcus, to form the central (Rolando's) sulcus of the Apes. The rest of the coronal forms the sulcus rectus of the Apes.

The point which I wish to specially emphasise in these notes is the fact that the suprasylvian sulcus is the most stable and morphologically fixed feature on the outer surface of the neopallium. So that the supposition that this sulcus alone (of all the common sulci of the Carnivora) is unrepresented in the Primates, as Ziehen and most recent writers would have us believe, is utterly inconceivable.

The so-called "Sylvian fissure" of the Carnivora, Ungulata, and other non-primate Orders is an exceedingly variable and unstable furrow, which can in no sense be regarded as the homologue of the Primate Sylvian fissure. The brain of *Chiromys* clearly demonstrates that the Prosimian Sylvian fissure may become broken up into two furrows, the more dorsal of which is obviously and unquestionably the suprasylvian sulcus, and the other is the analogue of the unstable feline type of pseudosylvian sulcus. Even if we had not *Chiromys* so clearly to point the way to the solution of this problem, nor even the striking demonstration of the tendency toward the forma-

tion of the Primate type of Sylvian fissure exhibited in the Edentata (*Myrmecophaga*), Rodentia (*Dolichotis*), and especially in the Arctoid Carnivora, the fact that the suprasylvian sulcus is the most stable and precocious furrow in the Mammalia naturally suggests the possibility that it may represent or take some share in the formation of the furrow which is also the most stable and precocious sulcus in the brain of the Primates, in other words, the "Sylvian fissure."

Many writers have appreciated the difficulty of accounting for the suprasylvian sulcus in the Primates, but hitherto no one has suggested the interpretation, which is, I am convinced, the true explanation of its fate.

Such a suggestion will be regarded by most comparative anatomists as utterly preposterous; but before they express such views I would recommend them to study the development of the sulci in any of the common mammals, to examine the condition of the "Sylvian group" of sulci in such mammals as the Arctoidea (*e.g.*, *Ictonyx* and *Meles*), and, after this preparation, to investigate carefully the constitution of the "Sylvian fissure" in a series of Primates, not neglecting the genera *Lemur*, *Callithrix*, *Hylobates* and the Gorilla.

If this course be followed I believe that every unbiassed observer must admit that the stability of the Primate "Sylvian fissure" is wholly due to the fact that the suprasylvian sulcus is incorporated in this peculiar combination of sulci. The *form* of the "fissure" is, however, chiefly determined by the pseudo-sylvian sulcus.

The problem of the causation of the stable sulci I shall not discuss at present. This much, however, is certain, that such furrows as the calcarine, suprasylvian, orbital, coronal, and lateral cannot be produced as the expression of (in other words, to relieve the tension produced by) a mere *general* expanse of the neopallium. They are in all probability caused by the unequal growth of neighbouring areas of different physiological significance, just as the rhinal fissure is produced by the unequal expansion of the neopallium and the pyriform lobe.

But once a furrow is formed, it is only natural that it should be made use of in the process of folding which takes place to accommodate the expanding neopallium.

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and to increase in depth and morphological limits (if such a cortex grows. So that, in comparison with that of another brain, the extent of one sulcus corresponds to the extended form of a furrow; that the fundamental elements are the same.

It is this obvious limitation to the most of the confusion in the following as a necessary condition to compare convolutions and different orders the mechanism of the secondary extensions and the divergent effects in the

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ON THE SUCCESSION AND HOMOLOGIES OF THE MOLAR AND PREMOLAR TEETH IN THE MAMMALIA. By H. W. MARETT TIMS, B.A. (Camb.), M.D., M.Ch. (Edin.), *King's College, Cambridge.*

THE anomaly in the nature of the tooth-change in the posterior premolar region of many mammals is well known to all Comparative Anatomists. It lies in the fact that while the anterior milk premolars are succeeded by teeth of like pattern, and which develop behind them, the posterior successional premolar develops in front of its predecessor, which is distinctly molari-form.

This peculiarity is one of great antiquity, as evidenced by its occurrence in certain of the Mesozoic vertebrata, *e.g.*, *Triconodon*. Among existing mammals it is to be met with in individual members of at least four Orders, viz., Marsupialia, Carnivora, Insectivora and Rodentia.

Such a succession and one of so great antiquity cannot be regarded as a mere coincidence, or explained in the same way as that occurring in other regions of the jaw. Any discussion upon this subject must centre around the tooth-change in the marsupials, since in them the posterior premolar is the only tooth to be replaced, and therefore the conditions would appear to be less complicated than in other mammals.

Recent investigations tend to show that a truly monophyodont condition is not yet present in the mammalia, except possibly in the Monotremata. Scarcity of material has hitherto prevented the tooth-genesis from being worked out in them, but Professor Poulton has drawn attention to the presence of spherical epithelial bodies on the labial side of some of the teeth of

Ornithorhynchus (6). His description of these agrees closely with that of similar structures observed in relation to certain of the cheek-teeth in *Canis*, *Cavia* and *Gymnura*. I have elsewhere (14) expressed the opinion that they possibly represent the last stage in the disappearance of pre-existing teeth. Should this be the correct interpretation, then the *Monotremata* also must be regarded as at least diphyodont.

The researches of Leche, Kükenthal and others have led to the assumption that the functional teeth of the Marsupials correspond morphologically with the milk dentition of the *Eutheria*, but I have previously (12) adduced reasons for homologising the marsupial dentition with that of the replacing set of other mammals, thus reverting in part to the discarded views of Flower and Oldfield Thomas.

Several writers have described what they conceive to be vestiges of an additional premilk series in such animals as Man, Ox, several Rodents, and Pig. I hesitate to accept fully the interpretation which has been placed upon these appearances, for such labial downgrowths of the dental lamina are frequently to be noticed in very young jaws which, when traced through later stages, seem to form the enamel epithelium of the external cingulum. On theoretical grounds the evidence of a premilk dentition would be welcome, as it would be further proof of a polyphyodont ancestry. However, the presence or absence of such does not affect the views expressed as to the homology of the marsupial dentitions.

Since the publication of these opinions they have been adversely criticised by M. F. Woodward and, at considerable length, by Deppendorf (2). Both these investigators base their objections on, as it seems to me, too purely theoretical grounds. The former, referring to my conclusion, writes (20),—"It will no doubt be difficult to convince such believers that their interpretation is incorrect until we can find some premilk teeth in the *Placentalia* better developed than those of Leche and Röse, and we can only admit that ontogeny is not as conclusive on the point as one could wish, but I think, on phylogenetic grounds, based partly on palæontological evidence, and on the general consideration of the supposed evolution of the sucking Mammals, with their reduced dentition, from the egg-laying reptile, with

its polyphyodont dentition, we are forced to the conclusion that a small set of teeth must have existed, and has since been lost (or almost so) during that evolution, and of this set the last traces are seen in the premilk dentition." Deppendorf argues in a similar manner, pointing to the reptilian descent of the marsupials as affording an inherent argument for the retention of the earlier dentition.

Admitting the truth of the hypothesis of reptilian descent, the conditions of life in young marsupials are very different from those of the newly hatched reptiles. Though born in a very rudimentary state, the young remain in the pouch for a considerable time, fed by milk compressed from the maternal mammary glands; whereas reptiles, though able to forage for themselves from the time that they leave the egg, having already a complete fully formed and erupted dentition, are hatched in a much more advanced condition. These considerations appear to me rather to controvert the conclusions of Woodward and Deppendorf, and to favour the view that the earlier dentitions would tend to be retained in the Reptilia, and to be suppressed in the Marsupialia. Moreover, the objections urged are in no way applicable to the Cetacea, in which the dentitions are similar to those in the marsupials, and to which I would apply similar interpretations.

Proceeding to a consideration of the tooth replacement in the molar and premolar regions, it is well known that pm. 1, when it exists as a functional tooth, is represented in one dentition only in a number of mammals, for example Hyrax, the Indian Tapir, Dog, and occasionally the Pig. Adopting the same line of argument, and believing that the whole trend of evidence is towards the view that the mammalian dentitions are tending to disappear from without inwards, as shown by the gradual suppression of the milk teeth, I would refer the pm. 1 of these animals to the persistent series. Upon like grounds, I also interpret the molar teeth, thus agreeing with Woodward, Lataste and Magitot, but differing from the conclusions of Owen, Hoffmann, Beauregard, Kükenthal, Leche and others.

The point to which I wish to draw attention is the method of tooth replacement in the posterior premolar region, the

anomalous character of which has already been pointed out. A consideration of this subject naturally suggests two questions:—

1. Is the replacing tooth in this position the true morphological successor of the deciduous molariform tooth? If not, what is the nature of the replacement, and what may be the determining causes?

2. Are the hindmost teeth of the premolar series in the Marsupials, Carnivores, Insectivores, and Rodents homologous.

Wilson and Hill (15), after a study of the tooth-genesis in *Perameles*, quite independently arrived at the same conclusion as I had done, that the functional teeth of the marsupials belong to the successional series; but they believe the "deciduous premolar to be a true milk tooth, and not the sole representative to which it belongs, since the so-called pre-lacteal teeth are in reality milk teeth which have undergone reduction and have well-nigh disappeared under the operation of influences unfavourable to their development." These authors therefore believe the replacing tooth to be a true morphological successor.

Woodward's researches into the tooth-genesis in the Kangaroos led him to the opposite conclusion: he found (18) that in these animals "the one functional successional tooth is never by any chance developed from the fourth premolar; and although it displaces that tooth along with the third, it is not the representative of the same [pm. 4] of the second dentition." This successional tooth, he further says, "arises independently of the 3rd and 4th premolars from the dental ridge connecting these two teeth," and by the great development of the latter the dental lamina of the successional tooth appears as if it were a "downgrowth from the inner side of the enamel-organ of pm. 4," consequently he thinks the replacing tooth belongs to the same series as pm. 3, and pm. 4.

This view was not accepted by Leche (4); but, in the light of the further evidence forthcoming from Woodward's additional investigations into the origin of the teeth in the Insectivores (19), and from the fact that it accords so completely with what has been observed in the Dog, I think there is sufficient justification for its adoption.

Wilson and Hill make no mention of any such condition in *Perameles*; and though I have not noticed any definite statement in their lengthy monograph, the general impression conveyed is that d.p.m. 4 and p.p.m. 4 are morphologically connected. If, however, their paper be examined more critically, it is by no means clear that such is the case. It is true that they describe and figure a well marked downgrowth of the dental lamina to the lingual side of d.p.m. 4. [d.p.m. 3.]; this downgrowth is traced until the usual bell-shaped stage is reached, but in some of the figures it appears (*e.g.*, fig. 67) to be much smaller relatively to the size of the other teeth than in the earlier stages, the authors speaking of the "distinct though small papilla" of pm. 3 [pm. 4] in their stage 10. Nothing is stated to show that, later on, this rudimentary germ actually develops into the functional tooth. A similar downgrowth is noted by Woodward in several instances (18, 20), and in these has been found *not* to give rise to the successional tooth. Attention may be drawn to the fact that mention is made of the presence of "a very striking example of cell-nest formation" in connection with the anlage of pm. 3 [pm. 4], near to the oral epithelium. Reference has already been made to the importance attaching to such structures in determining serial homologies.

Again, though the lingual downgrowths appear to develop towards the posterior part of d.p.m. 4, its successor erupts in front of it, as mentioned and figured by the joint authors, but they do not appear to have noted it as being exceptional; although this is in fact unusual throughout the mammalia except in the case of this particular tooth, where it is the rule not only in the marsupials, but also in the other three orders of the Placentalia under consideration. Woodward is very explicit upon this point, for he says, "It is interesting to note that in *Perameles* the large supposed successional tooth is quite distinct in origin from the small 4th premolar which is shed; it is in fact formed from the dental lamina situated immediately behind pm. 3, and morphologically in front of the 4th premolar. Further, if a skull be examined in which the teeth-change is taking place, it will be seen that the supposed successor of the 4th premolar cuts the gum in front of that

tooth to which it is believed to be its milk predecessor" (18, pp. 467-8).

Reference is also made by them to the condition in *Phascolarctos*; and Leche's figures, in which both p.d. 3 and p. 3 are represented, are reproduced. Similar criticisms are, I think, applicable, as in the case of *Perameles*; moreover, Woodward, in an examination subsequent to the publication of Leche's original work, found that the successional premolars above and below develop "well in front of d.p.m. 4" (*loc. cit.*). Without entering further into this discussion, it would appear that the authors' attention had not turned to this particular, other objects being in view. From what can be gathered, it seems possible, if not probable, that *Perameles* will be found to fall into line with the many other marsupials examined by Woodward.

In a previous paper (13) I have attempted to show that the same holds good in the Dog, as representative of the Carnivora; and Woodward finds it to be true also for several of the Insectivora. Among the Rodents the so-called p.p.m. has been shown not to be the morphological successor of d.p.m. (14), but to belong to the same series, and to develop in front of it.

Such being the case, it becomes necessary to find out if possible what the successional and deciduous teeth really are, the nature of the tooth-change, and its possible causes. It has been shown that in the Dog and Guinea-pig both d.p.m. 4 and p.p.m. 4 belong to the replacing series, the latter developing in front of the former. The deciduous tooth I also believe to be the anterior member of the true molar series, all of which I regard as belonging to the second dentition.

In dealing with the Insectivores, Woodward found a similar condition, but interpreted it in a somewhat different manner. He describes the p.p.m. 4 as developing in front of d.p.m. 4: the latter, he says, is the "only true deciduous molar"; the p.p.m. 4, however, he regarded as "really the milk, but non-deciduous 4th premolar."

Now this writer is, as he practically admits, under the influence of his previous conclusions as to the tooth replacement

in the Macropodidæ. If his statements be compared, there will be found to be some discrepancy, for he says (19, p. 580) that in *Macropus* p.pm. 4 "was evidently serially homologous" with d.pm. 3 and d.pm. 4. Now the latter tooth he regarded as being "the first true molar accelerated," and he frequently expressed the opinion that the true molars belong to the replacing dentition; he also shared the general opinion that the anterior premolars of the marsupials belong to the milk series. Clearly, therefore, p.pm. 4 cannot be serially homologous with both d.pm. 3 and d.pm. 4. The p.pm. 4 of the Insectivores he likewise considered to be a milk tooth, but since no mention is made of any downgrowths of the dental lamina in connection with that tooth, one can only presume that this conclusion was arrived at upon the basis of his interpretations of the teeth of marsupials. From the evidence of the facts, I am of the opinion that p.pm. 4 of the Insectivores belong to the replacing series as in the Dog and Guinea-pig.

Leche, even after a consideration of these views of Woodward, appears still to regard p.pm. 4 as the true morphological successor of d.pm. 4, even though of an entirely different pattern, a conclusion which I think no longer tenable. It may be convenient here to give a resumé of the various conclusions relating to the marsupials above mentioned:—

1. That the deciduous tooth is a true milk tooth, and p.pm. 4 its morphological successor, the former being in series with all the other teeth, and belonging to the milk dentition (Leche).

2. That the deciduous tooth in *Perameles* is a true milk tooth, and presumably the p.pm. 4 its morphological successor; the latter is in series with all the other teeth, and belonging to the replacing dentition (Wilson and Hill).

3. That the deciduous tooth is the first true molar, and therefore of the replacing dentition, while the p.pm. 4 is not the morphological successor, but a milk tooth in series with the antemolars only of the marsupials (Woodward).

4. That all the teeth of the marsupials, including d.pm. 4 and p.pm. 4, belong to the permanent dentition; the deciduous tooth being the first tooth of the true molar series (Tims).

Views as to the tooth-change in this position in the Eutheria:—

1. That d.p.m. 4 is in reality m. 1, *i.e.* a tooth of the second dentition, while p.p.m. 4 is in reality d.p.m. 4, *i.e.* a tooth of the first dentition. (Woodward, for the Insectivora.)

2. That d.p.m. 4 is really m. 1, *i.e.* a tooth of the second dentition, while p.p.m. 4 is really the morphological p.p.m. 4, *i.e.* a tooth also belonging to the second dentition. (Tims, for Carnivora, Rodentia, Insectivora and Marsupialia.)

If the view here enunciated be accepted, then the peculiar method of tooth-replacement in this position is identical in every known instance, and all complication disappears. It would appear to afford further presumptive argument in favour of the functional teeth of the marsupials being the homologues of the replacing dentition.

The peculiarity of this replacement appears to be the outcome of overcrowding of the teeth in the jaw. This may have been brought about in one of three ways; viz., (*a*) by an actual shortening of the jaw, (*b*) by an antero-posterior increase in the length of the teeth in relation to the length of the jaw, or (*c*) by these two factors acting concurrently.

Woodward believed that the peculiarity of the tooth-change might possibly be due in part to a shortening of the jaw, but chiefly to an increasing development of the successional tooth. This view derives support from a statement by Oldfield Thomas (10) that in *Phascologale* the milk premolar varies in size and persistency according to the development of p.p.m. 4, being large and long persistent in the species with large p.p.m. 4, and small or altogether absent in the others. In order to test these hypotheses I have worked out the accompanying tables,—the Facial Indices having been already worked out by Thomas. The figures express the ratios of the Basi-facial axis (*i.e.*, from the Sphenoidal suture to the Gnathion) and other measurements to the Basi-cranial.

It must be remembered that great diversity exists within the limits of the Marsupialia as to the age at which the milk tooth is shed, and consequently as to the extent to which it is functionally active. Precise information on this point is difficult to obtain, and indeed in only a comparatively few instances is the

approximate age known. Scattered and indefinite statements are to be found in the literature, but the fullest and most reliable are to be found in Mr Oldfield Thomas' "Catalogue of the Marsupialia and Monotremata in the Collection of the British Museum (Natural History)."

I have collected all the cases in which the measurements of adult or immature and of aged specimens have been given by Oldfield Thomas, in order to ascertain if there be any constancy in the relative increase or decrease of the essential parts of the skull with advancing age. In the first place, it will be seen that there is an *increase* in the facial index and palatal length in all forms except in *Petaurus*, *Trichosurus* and *Perameles*. The diminution in the facial index in *Petaurus* is exactly compensated by that of the palate, therefore it is clear that there must in this animal be a relative shortening of the jaw in the passage from adult to old age, whereas in *Trichosurus* and *Perameles* the difference in palate length is not an equivalent to that of the facial index, from which it is to be inferred that in both these forms there is an additional relative shortening of the sphenoidal portion of the skull. Presuming similar changes to have taken place in passing from infancy to adult life in these forms, in which we have the opposite extremes, as well as a mean age for shedding of the milk tooth, it would not appear that a mere shortening of the jaw in relation to the basi-cranial axis is the sole determining factor.

In *Dasyurus* and *Didelphys* these relative measurements remain unaltered in the passage from adult to old age.

Concomitantly with these changes there appears to be a constant diminution in the palatal breadth, except in *Onychogale*, and to a negligible extent in *Phascolarctos* and *Dasyurus*. This table, therefore, furnishes no definite explanation, but it is interesting to note that in all these marsupials there is a general tendency to proportionate increase in the length and diminution in the breadth of the jaws with increasing age. This is shown in the column in which I have worked out the ratio of the breadth to the length, the only exceptions being *Trichosurus* and *Perameles*, in which the decrease is very slight, and in both these forms the deciduous tooth is shed

TABLE I.—Comparison of Adult or Immature with Aged Marsupials.

	Facial Index.	Palate Length.	Palate Breadth.	Length of p. 4.	Length m.s. 1.3.	Ratio of Palate, Breadth to Length.	Ratio of Molar Length to Palate Length.
DIPROTODONTIA.							
<i>Macropodidae.</i>							
<i>Macropus giganteus</i> (adult),	269	252.3	116.6	...	79	1 : 2.1	1 : 3.2
" (aged),	276	262.8	100	...	67	1 : 2.6	1 : 3.9
<i>Macropus rufus</i> (immature),	276	246.9	113.5	...	93.8	1 : 2.1	1 : 2.6
" (aged),	311	284.4	112.2	...	77.7	1 : 2.5	1 : 3.6
<i>Onychogale lunata</i> (immature),	200	176.7	93	...	67.9	1 : 1.9	1 : 2.6
" (aged),	215	190	101	14	68.5	1 : 1.8	1 : 2.8
<i>Lagorchestes conspicillatus</i> (adult),	206	185.1	104.8	28.8	68.3	1 : 1.7	1 : 2.4
" (aged),	214	194.4	103.1	27.3	71.4	1 : 1.8	1 : 2.7
<i>Phalangeridae.</i>							
<i>Petaurus breviceps</i> (adult),	182	161.9	89.5	14.9	44.7	1 : 1.7	1 : 3.6
" (old),	174	153.2	82.2	15.3	43.4	1 : 1.8	1 : 3.5
<i>Trichosurus vulpecula</i> (adult),	189	171.4	90.2	18.7	55.2	1 : 1.9	1 : 3.1
" (old),	178	159.2	88.8	16.6	50.3	1 : 1.7	1 : 3.1
<i>Phascogale cinereus</i> (adult),	191	152.2	81.8	17	49.3	1 : 1.8	1 : 3.09
" (aged),	214	168	81.9	15.5	51.4	1 : 2.05	1 : 3.2
POLYPTODONTIA.							
<i>Peramelidae.</i>							
<i>Perameles macrura</i> (adult),	227	212	93.6	13.6	52	1 : 2.2	1 : 4.07
" (aged),	208	186.4	88	14	49.2	1 : 2.1	1 : 3.7
<i>Dasyuridae.</i>							
<i>Dasyurus hallucatus</i> (adult),	193	170.7	96	...	65.3	1 : 1.9	1 : 2.6
" (aged),	193	170.7	96.1	...	65.3	1 : 1.9	1 : 2.6
<i>Didelphyidae.</i>							
<i>Didelphys marsupialis</i> (adult),	223	197.1	89.8	15	51.5	1 : 2.1	1 : 3.8
" (aged),	223	197.5	78	19.5	43.4	1 : 2.5	1 : 4.5
<i>Didelphys dimidiata</i> (adult),	197	165.2	86.5	...	43.4	1 : 1.9	1 : 3.8
" (aged),	195	165.3	81.5	...	40	1 : 2.2	1 : 4.1

The actual measurements upon which this and the following table are based are given in Mr Oldfield Thomas' "Catalogue of Marsupials." The numbers given above express these measurements in terms of the Basal-cranial axis, which has been taken as 100.

about the same period of life, while in *Dasyurus*, where the proportions remain unchanged, the tooth is shed early. These facts acquire an additional importance in view of the opinion of Winge (16, 17) and Woodward (19) as to the secondary lengthening of the jaw in *Macropus* and other long-nosed forms.

Obtaining no very satisfactory results from this table, I next proceeded to work out in the same manner the measurements of the adult forms of all these marsupials about which I had been able to obtain more or less definite statements as to the approximate age at which the milk tooth is shed. These results are set forth in Table II. The genera in both Diprotodontia and Polyprotodontia are arranged according to the period of shedding, the first in each list retaining its milk premolar the longest. I would explain in passing the meaning of the two sets of figures given for *Peragale lagotis*. The measurements given by Oldfield Thomas were all from 'aged' specimens, and therefore not quite suited for purposes of comparison. I therefore estimated the average differences found to exist between 'adult' and 'aged' members of the Peramelidæ in Table I., and in that way 'corrected' the ratios for the adult.

A glance at the table shows that though there is a progressive diminution down the list of Diprotodonts in both palatal length and breadth to the basi-cranial, no such regularity is to be found in Polyprotodonts; *Sarcophilus*, with its absence of both d.p.m. 4 and p.p.m. 4, having a slightly greater palatal length than *Didelphys*, in which the deciduous tooth remains in place till the animal has nearly reached maturity. It will also be seen that neither the horizontal length of pm. 4 nor of ms. 3 bear any relation to the age at which the tooth is shed. Failing to find any explanation in these, I worked out the ratios between the palatal length and breadth, and in this I think is to be found a satisfactory basis. This column shows an almost unbroken sequence for both Di- and Poly-protodonts, the exceptions being *Thylacinus* and *Sminthopsis*. Possibly an explanation for these is to be found in the very specialised dentitions present in these two genera.

Notwithstanding these exceptions, the table is sufficiently

TABLE II.—Comparison of Adult Forms.

	Facial Index.	Palate Length.	Palate Breadth.	Length of p. 4.	Length m.s. 1-3.	Ratio of Palate, Breadth to Length.	Remarks.
<i>Diprotodontia.</i>							
<i>Macropus magnus</i> ,	276	253.6	116.3	17	78.7	1 : 2.1	Milk premolar well developed and long persistent (Oldfield Thomas).
<i>Trichosurus vulpecula</i> ,	189	171.4	90.2	18.7	55.2	1 : 1.9	Persistent long enough to be of service (Oldfield Thomas).
<i>Phalanger orientalis</i> ,	175	159	86.7	16	44.1	1 : 1.8	Reduced to a minute rudiment, apparently functionless (Oldfield Thomas).
<i>Phascogale cinereus</i> ,	191	152.2	81.8	17	48.9	1 : 1.8	Not yet found. Probably minute and early deciduous (Oldfield Thomas).
<i>Dromicia nana</i> ,	164	144.4	83.3	18.8	44.4	1 : 1.7	
<i>Polyprotodontia.</i>							
<i>Myrmecobius fasciatus</i> ,	211.8	223.5	70.5	1 : 3.1	Not known.
<i>Perameles macrura</i> ,	227	212	93.6	13.6	52	1 : 2.2	Persists till animal is 3 grown (Wilson and Hill).
<i>Charopus castanotis</i> ,	256	243.3	110	18.6	72	1 : 2.2	Milk p. 4 present and functional (Oldfield Thomas).
<i>Perigale lagotis</i> (aged),	255	232.4	107.5	13.5	51.6	1 : 2.1	Large functional and long persistent (Oldfield Thomas).
" corrected for adult, {	274	258	113.1	12.9	54.4	1 : 2.2	[[Flower and Lydekker].
<i>Didelphys marsupialis</i> ,	223	197.1	89.8	15	51.5	1 : 2.1	Remains in place till animal is nearly adult
<i>Thylacinus cynocephalus</i> ,	290	218.6	107.5	19.3	67.9	1 : 2.03	Shed before the animal leaves the mother's pouch (Flower and Lydekker).
<i>Phascogale wallacei</i> ,	200	170.6	97.3	13.3	61.3	1 : 1.7	Persists longer in those forms with large p. 4. This is the largest measurement given by Oldfield Thomas.
<i>Sminthopsis leucopus</i> ,	196	168.1	103.4	15.9	52.2	1 : 1.6	Large and long persists
<i>Dasyurus viverrinus</i> ,	210	185.1	111.1	...	69.1	1 : 1.6	Constantly present in (Wilson and Hill).
<i>Phascogale apicalis</i> ,	185	164.5	103.6	6.3	19	1 : 1.5	The sp. with small p. 4
<i>Antechinus laniger</i> ,	179	146	93.2	15.7	49.4	1 : 1.5	Not known. † same as Thomas).
<i>Sarcophilus ursinus</i> ,	224	197.3	103.1	...	92.6	1 : 1.2	d.p.m. 4 and p.p.m. 4 both absent (Oldfield Thomas).

striking to afford some justification for the belief that the peculiarity of the tooth-change and the age at which it occurs is due not to an actual shortening of the jaw in relation to the basi-cranial axis, but to a *shortening of the length of the palate in relation to its breadth*.

I have included the proportions for *Myrmecobius fasciatus*, and it will be noticed that the palatal length is more than three times the breadth, and that for an 'adult,' and not an 'aged' specimen. This is considerably greater than that of any other marsupial, or indeed of any other mammal that I have yet measured. The conclusion suggests itself either that in *Myrmecobius* there is no deciduous premolar, or if there be, that it is shed very late in life. Oldfield Thomas (10) remarks that the milk premolar is 'as yet unknown.' It is true that both Leche and Woodward have examined pouch embryos from the same batch, and the latter 'several much older specimens' also, but gives no clue as to their age or size; from the descriptions they were none of them very advanced. Woodward speaks (20) of the 'supposed successors,' from which it would seem that he had not been able to trace the actual replacement. Thus, in the absence of evidence to the contrary, I am inclined to adopt the former alternative, and to believe that there is no deciduous premolar.

It is well known that *Myrmecobius* possesses at least five upper molars, a number in excess not only of other marsupials but of all other mammals. It seems possible to suggest that the anterior molar in this animal is the homologue of the deciduous tooth of other marsupials; the shortness of the jaw in the latter producing a kink in the dental lamina, and causing the anterior molar to be pushed over the crown surface of the tooth in front of it, and thus appearing as its morphological predecessor. The greater length of the jaw in *Myrmecobius* has allowed the development of the teeth in their normal primitive positions, and produced no overlapping of the teeth. If this be the correct interpretation, it follows that the so-called m. 1 of the marsupials generally is the homologue of m. 2 of *Myrmecobius*. The suggested tooth relationships are shown in Scheme A., the missing premolar being taken as pm. 2, according to Oldfield Thomas' identification (9).

SCHEME A.—*Marsupialia*.

Type,	V	V	V	V	U	U	U	U	U	U	+
Myrmecobius,	V	.	V	V	U	U	U	U	U		
Thylacinus,	V	.	V	V U	.	U	U	U	U		
Dasyurus,	V	.	V	V U	.	U	U	U	U		
Sarcophilus,	V	.	V	.	.	U	U	U	U		
<hr/>											
Macropus and Trichosurus,	.	.	V	V U	U	U	U	U	U		
Phalanger,	v	.	v	V u	U	U	U	U	U		
Phascolarctos,	.	.	.	V u	U	U	U	U	U		
Dromicia,	v	.	v	V	U	U	U				

The explanation offered by Winge of the dentition in *Myrmecobius* accords more nearly with the interpretation here suggested than that of any other writer. He believes the deciduous tooth to be the morphological predecessor of p.p.m. 4, "but that it remains in place *behind* its successor, and owing to the length of the jaw is not shed, functioning along with the other teeth. He says "den lille mælke Kindtand, d.p. 3, bliver ikke fortrængt af sin Afloser p. 3, men Afloseren bryder form foran den" (17, p. 91). The length of the jaw Winge regards as secondary. With these conclusions Deppendorf (2) agrees.

TABLE III.—*Showing the Ratios of the Palatal Breadth to Length in some of the Insectivora.*

<i>Centetes ecaulatus</i> [young, 1 : 2·47]					
[old, . 1 : 3·05]					
mean for adult,		.	1	:	2·76
<i>Gymnura rafflesii</i> ,	1 : 2·13
<i>Sorex araneus</i> ,	1 : 1·80
<i>Talpa europæa</i> ,	1 : 1·6
<i>Ericulus nigrescens</i> ,	1 : 1·61
<i>Echinops telfairi</i> ,	1 : 1·5
<i>Erinaceus occidentalis</i> ,	1 : 1·47
<i>Solenodon cubanus</i> ,	1 : 1·12

In Table III. will be found the ratios of the palatal breadth to the length occurring in certain Insectivores, the tooth-genesis of some of which have been investigated by M. F. Woodward (19). In the forms which he examined he found that pm. 4 develops in front of d.pm. 4 with the exception of *Sorex*, in which the successional tooth develops lingually to its predecessor. I desired therefore to see whether the measurements in this animal corresponded with this peculiarity, but they do not. From the evidence at hand it does not seem safe to draw any decided negative conclusion, since Woodward was only able to examine one stage, and as the number of deciduous cheek-teeth in the Shrews varies, as shown by Tauber (8); and as Woodward identifies as pm. 1 the tooth which Brandt (1) and others usually regard as a Canine, it cannot be regarded as settled that in *Sorex* we really have to deal with an exceptional method of tooth-replacement in this position. Though Leche has also examined the development of the teeth in this animal, he has not regarded it from this point of view. A study of this table would seem to suggest that further investigation of later stages might show that *Sorex* is no exception to the other genera of Insectivores examined by Woodward.

It will also be seen that *Centetes* has the greatest palatal length, and it also possesses one molar in excess of other Insectivora, as shown by Oldfield Thomas (11); its dentition is therefore comparable to that of *Thylacinus*, except that its two anterior premolars are replaced. It is of interest to compare the measurements of *Centetes* with those of *Solenodon* in relation to the question of tooth homologies. Oldfield Thomas draws attention to certain dental differences in the two families. In the *Centetidae* both d.pm. 4 and p.pm. 4 are "absolutely molariform," while d.pm. 3 and p.pm. 3 are "functionally carnassial." In the *Solenodontidae* the posterior premolar which Thomas identifies as pm. 4 is functionally carnassial, and the penultimate premolar identified as pm. 3 being "absolutely premolariform"; the missing premolar he believes to be pm. 2. A comparison of the measurements would seem to suggest that both d.pm. 4 and p.pm. 4 are wanting; it is in fact in a similar condition in regard to this tooth as is *Sarcophilus* among the marsupials, with which the ratios of the measurement exactly

correspond. If this be so, then the carnassial tooth of *Solenodon* is the homologue of the carnassial of *Centetes* pm. 2, in both cases being premolariform and the successional tooth in each instance of like pattern to its predecessor. The relationships of the teeth of some of the *Insectivora* as here suggested are shown in Scheme B.

SCHEME B.—*Insectivora*.

<i>Centetes</i> ,	.	V	V	V	U	U	U	U	U
		v	v						
<i>Ericulus</i> ,	.	V	V	V	U	U	U	U	
		v	v						
<i>Echinops</i> ,	.	V	V	V		U	U		
		v	v	u					
<i>Solenodon</i> ,	.	V	V	.	U	U	U		
		V	v	v					

In Tables IV. and V. are given the ratios of the palatal measurements of the Dogs and Rodents. In the former, *Otocyon*, with its additional molar, is at the top of the series. A few of the *Felidæ* are added for comparison. It is quite possible that the measurements given for the Rodents may prove value-

TABLE IV.—*Showing the Ratios between the Palatal Breadth and Length in some Carnivora.*

CANIDÆ.	<i>Otocyon megalotis</i> ,	1 : 2·1
	Average for dogs generally varies from	1	:	1·7	to	1 : 1·5	
	<i>Icticyon venaticus</i> ,	1 : 1·3
	<i>Cyon rutilans</i> ,	1 : 1·2
FELIDÆ.	<i>Felis pardalis</i> ,	1 : 1·17
	<i>F. macrocelis</i> ,	1 : 1·14
	<i>F. yaguarandi</i> ,	1 : 1·03
	<i>F. serval</i> ,	1 : 1·02
	<i>F. catus</i> ,	1 : 0·97
	<i>F. domesticus</i> ,	1 : 0·96

less, owing to the peculiar conformation of the palate; nevertheless, since the anomalous method of tooth replacement has been noted in the Guinea-pig alone, it may be of some advantage to give the ratios for future guidance in the investigation of this subject.

TABLE V.—*Showing the Ratios between the Palatal Breadth and Length in some Rodentia.*

<i>Anomalurus pietii</i> ,	1 : 3·23
<i>Mus decumanus</i> ,	1 : 3·00
<i>Mus rattus</i> ,	1 : 2·93
<i>Hystrix leucura</i> ,	1 : 2·69
<i>Cavia guianæ</i> ,	1 : 2·2
<i>Sciurus vulgaris</i> ,	1 : 2·11
<i>Sciurus ephippium</i> [Borneo],	1 : 1·76
<i>Lepus cuniculus</i> ,	1 : 1·75

It now remains to discuss the homology of the posterior premolar tooth in the Marsupials, Carnivores, Insectivores and Rodents. In so far as this question relates to the Carnivores there can be no doubt on the matter.

In the Marsupials the homology of this tooth with pm. 4 of other mammalia was first pointed out by Oldfield Thomas in 1887 (9). Since then considerable support has been derived from the researches of Woodward, who strongly favours this view. Thomas' conclusions only meet with qualified acceptance by Leche, Kükenthal, Wilson and Hill and others. The last mentioned authors in their joint paper adversely criticise them. They attach little or no importance to the occurrence of the rudimentary enamel germ which Thomas regards as representing pm. 2, even though Röse mentions the existence of a similar rudiment in *Didelphys*. The ground upon which they base their conclusion is, that Kükenthal was unable to confirm Röse's discovery in that animal, and that they "sought in vain for any confirmation (in *Perameles*)" of Thomas' view, appealing to Bateson's judgment as to the indefiniteness of evidence derived from tooth-variations. Though everyone will admit that there is much truth in Bateson's statement, nevertheless it appears to me that the quotation from his book on "Variation" upon which the joint authors rely may be urged with as much force against them as against the arguments adduced by Thomas. It is unlikely that observers of such high reputation as Oldfield Thomas, Röse and Kükenthal have been in error in the statements as to what they did or did not see, and the fact that the two former found rudiments of pm. 2 which were absent in

Kükenthal's specimen is only in accordance with what one might expect in a vanishing structure.

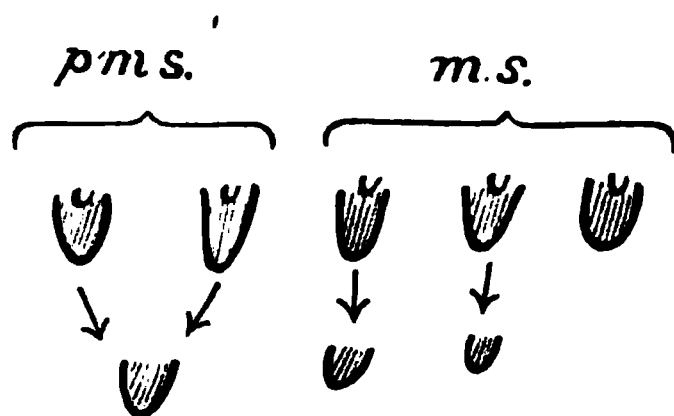
Further, the entire absence of the rudimentary enamel-germ in all Wilson and Hill's specimens of *Perameles* merely goes to show that the process of extinction has gone further in that Marsupial than in *Dasyurus* or *Didelphys*.

It appears to me, therefore, that no case has as yet been made out against Thomas' hypothesis. Moreover, the foregoing considerations as to the peculiar nature of the posterior premolar tooth-change in the four mammalian orders offers the strongest possible confirmation of that view, an argument which has not, so far as I am aware, been previously advanced in this connection. On these grounds there is, I think, ample justification for supporting the conclusions of Thomas and Woodward.

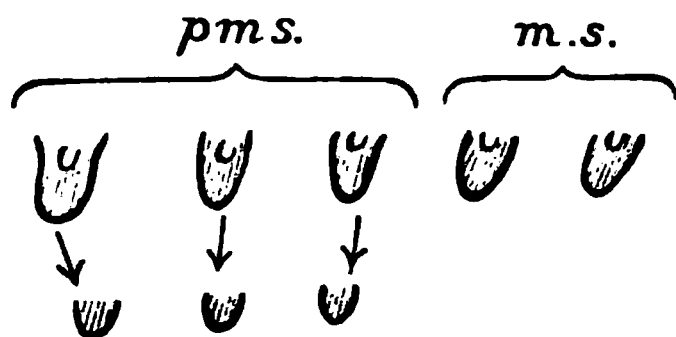
Turning now to the Rodentia, we enter practically new ground. Cuvier laid down the dictum, to which assent has very generally been given, that if a Rodent possesses more than three cheek-teeth, such teeth are to be regarded as premolars. In the Rabbit this may hold good, but not so in the Guinea-pig. I have drawn attention to the existence of concentric epithelial bodies in connection with the so-called p.p.m., m. 1 and m. 2 in the latter animal. Similar bodies have been mentioned as occurring in the Dog, *Gymnura*, *Perameles* and *Ornithorhynchus*. Such bodies present in so widely different animals cannot be without some morphological significance, and I have already given reasons for believing that they are to be regarded as the vestiges of pre-existing teeth. If such be the case, it follows that in *Cavia*, at any rate, either the accepted distinction between molars and premolars breaks down, or the dental formula is erroneous, in which case the Cuvier dictum falls to the ground.

Believing that the molars belong to the permanent series, it is quite conceivable, on theoretical grounds, that molar teeth did have at one time milk predecessors; indeed, the presence of labial downgrowths of the dental lamina in connection with developing molars have been noted in many instances. Nevertheless, with this reservation, the terms 'molar' and 'premolar' are distinctly useful as indicating a difference which exists at the present time among the greater number of mammals. If this

distinction is to be maintained, it then follows that the dental formula must be erroneous, since instead of one premolar and three molars, the reverse must be the case. Some light may be thrown upon their homologies by a study of the tooth-change in other Rodents. Dr Forsyth-Major (5) discusses this subject in various members of the Lagomidæ and draws attention to Fraas' statement as to the tooth-change in *Prolagus*. Fraas (3) gives the number of cheek-teeth in this animal as five in the upper jaw, with three deciduous molars; from the pattern, he regards the two anterior permanent teeth as premolars, the three posterior as molars, though the anterior two have milk predecessors. With regard to the tooth-change, Forsyth-Major quotes Fraas, who describes both the premolars as coming into place "through the same lacuna, produced by the dropping out of the first deciduous." This may be diagrammatically represented thus:—



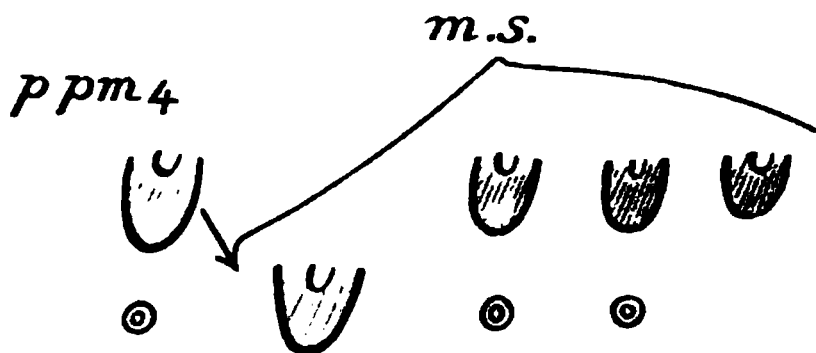
Forsyth-Major has examined two species, *P. beningensis* and *P. sardus*. He says, "the anterior of the three deciduous teeth is not situated directly above the anterior premolar but slightly backward, closely appressed to the second deciduous, so that with its anterior moiety it covers only the posterior part of the premolar; besides, it could not possibly cover the latter completely, being much smaller. It is needless to say that neither of the true molars supports a milk tooth." From this account the diagram would appear thus:—



The accounts given by these two authors agree in this important particular, namely, that the anterior successional tooth

drops backward to replace its predecessor in position, and presumably therefore develops in front of it. Now, this is precisely what has been seen to occur in some Carnivores, Insectivores and Marsupials, and the greatest credit is due to Fraas for having been the first to note the fact, though at the time he was unable, through lack of available knowledge, to appreciate its full significance.

In *Cavia* I have shown that a similar condition obtains, the successional tooth developing in front of the deciduous, and belonging to the same dentition, namely, the 2nd; and further, that in connection with three of the teeth, they are concentric epithelial bodies, to which reference has already been made. The condition is here represented:—



Comparison of this with the condition in *Prolagus* is very remarkable; in both the same striking peculiarity in the tooth-change is met with as in the other mammalian orders under consideration, the only difference between *Cavia* and *Prolagus* being that the two small posterior deciduous teeth of the latter have disappeared as such, and are only represented in the former by vestiges in the form of concentric epithelial bodies. One such body also occurs in relation to the most anterior tooth, but obviously being a microscopic structure, its presence or absence in *Prolagus* could not be determined; even were it present as a small tooth, its existence would be very easily overlooked.

From a consideration of these facts, it seems justifiable to establish the homology between the deciduous tooth and its successor in position of *Cavia* with the corresponding teeth of *Prolagus*; the two posterior deciduous teeth of the latter would then be the homologues of the two posterior concentric epithelial bodies of *Cavia*, of which they are the vanishing traces.

The question now presents itself, Is the anterior deciduous tooth of *Cavia* and *Prolagus* the homologue of d.pm. 4 of the other mammalia? To this it would seem impossible to give a positive answer. The presence of the diastema dates back to the lower Eocene for undoubted Rodents; and if, as I believe, the *Multituberculata* are to be regarded as the precursors of the Rodentia, then a diastema is to be found in those Mesozoic forms. It is but natural, therefore, that even the dental lamina may have now become lost as a continuous structure in the diastema of many existing Rodents, as shown by Freund. Such being the case, all traces of tooth vestiges in these regions are now lost to us for ever, and we can only look to Palæontology to furnish any possible evidence. The peculiarity of the tooth-change appears, however, to furnish strong presumptive evidence, which should not be overlooked. Additional evidence in favour of this view is furnished by Fraas, who says that the upper anterior deciduous tooth closely resembles the second of the permanent dentition, which is quite in accordance with the view that the deciduous tooth belongs to the permanent series, and is in fact m. 1, and therefore of like pattern to the second of the permanent dentition, which I would interpret as m. 2.

If the foregoing evidence be admitted as of any value, it then follows that in *Cavia* there are three molars, the two anterior of which have vestigial remains of predecessors, while in *Prolagus* there are five molars, two of which have small but definite milk predecessors.

The homology of the posterior premolar of the Insectivores with pm. 4 of the Marsupials and Carnivores presents some difficulty. As already stated, Woodward has demonstrated the fact of the development of the so-called pm. 4 anteriorly to its predecessor, but in the Centetidæ there is not the same difference in pattern between the two teeth, as both are distinctly molariform. It might be supposed that the shortening of the jaw in this family had produced the same sort of overlapping of the teeth, but affecting different members of the dental series, the m. 2 coming to occupy a position superficially to m. 1, and appearing as its morphological predecessor, thus accounting for the molariform pattern of both, and thus giving to Centetes

the large number of six molars and only two premolars, *Ericulus* and *Echinops* having five and four molars respectively. Though such a supposition seems possible, it is nevertheless simpler to regard the teeth involved as the homologues of d.pm. 4 and p.pm. 4 of the Carnivores and Marsupials, the latter tooth having become specialised and approximated in pattern to the molars, specialisation of this tooth being of frequent occurrence throughout the mammalia. One is urged to the acceptance of the latter alternative, since the adoption of the former would lead to endless confusion.

In conclusion, I wish to express my thanks to Professor G. B. Howes for various suggestions, and for drawing my attention to references in the literature; and also to Mr Oldfield Thomas for so kindly allowing me ready access to the Collection in the Natural History Museum.

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THE NORMAL POSITION OF THE BIG TOE.¹ By
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Hospital.*

FROM the above title it may perhaps be inferred that the big toe occupies a fixed position, but among Anatomists I need say no more in explanation than that by normal position I mean the usual lie of this digit. You are aware that this toe can be moved in a horizontal as well as in a vertical plane, that is to say, it can be abducted and adducted, as well as flexed and extended at the metatarso-phalangeal joint. But there is some doubt in the mind of the Anatomist, and especially in that of the Surgeon, as to what is the normal lie or position of this leading digit of the foot. Surgeons are told that the big toe should be straight and should lie in the direction of a line drawn from the inner side of the heel to the inner side of the joint of the big toe (Meyer, Ellis).

What grounds are there for this statement, and is it true? I venture to bring before you a series of data which you can easily verify for yourselves, and which demonstrate conclusively to my mind that this statement is contrary to fact, as the big toe is neither straight nor does it usually lie in line with the inner border of the foot.

The right and left big toes are asymmetrical and are not interchangeable with one another. The difference between the two is especially marked on examination of the phalanges, and it is not difficult to distinguish from a mixed collection of the phalanges of the big toe those which belong to the right from those which belong to the left.

The first phalanx of the big toe is asymmetrical, it being longer on its inner than on its outer border, in one specimen as much as 4 mm.; this asymmetry is well seen if the phalanx be taken and laid with its proximal end on a horizontal table, when not only the inequality in length of the two borders will

¹ Read before the February meeting of the Anatomical Society.

be seen, but the inclination of the phalanx to one side becomes obvious.

The direction of this inclination may be used to determine the side to which the phalanx belongs; for if this bone be set

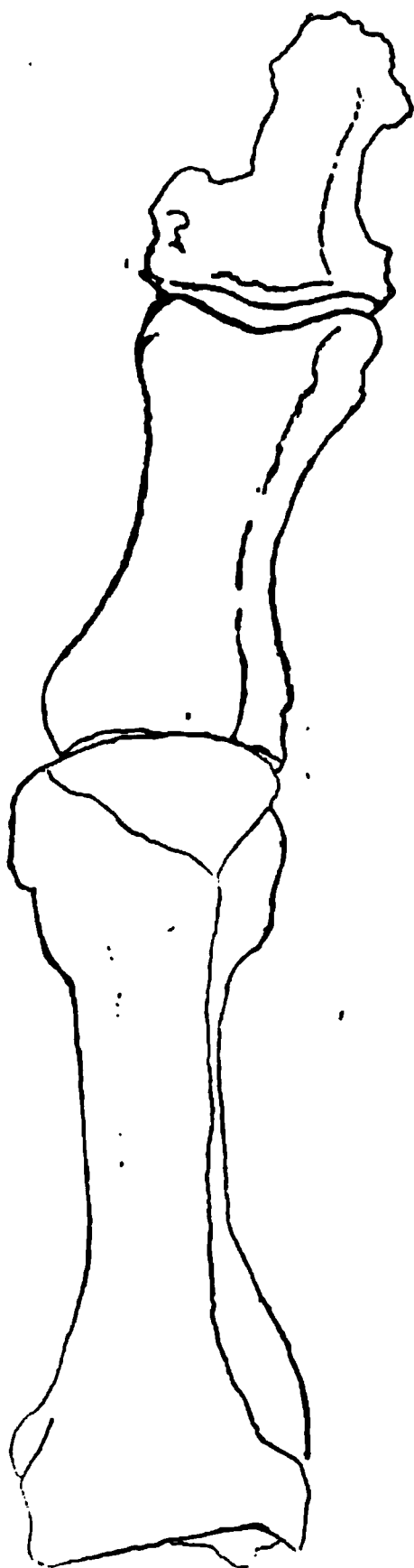


FIG. 1.—Dorsal view of phalanges of big toe and first metatarsal of right foot—(nat. size).

on its proximal end with its plantar surface forwards, it leans towards the side to which it belongs; that is to say, if the inclination be to the left, the bone belongs to the big toe of the left foot, and *vice versa*. In consequence of the inequality in length of the two sides, the distal articular surface is on a slant from within outwards and a little backwards.

The terminal phalanx is even more asymmetrical than the first, the inner border being longer than the outer; it inclines in the same direction, but even to a greater degree. The side

FIG. 2.—Horizontal section of phalanges of big toe and first metatarsal of left foot, showing disposition of lamellæ in each. In anterior end of the metatarsal the lamellæ run slantingly outwards, showing the direction in which first phalanx is pulled backwards upon the metatarsal.—(Nat. size.)

to which it belongs may be determined by the method above referred to in connection with the first phalanx.

The phalanges, when viewed from above, are not in line with one another, nor is the first a direct continuation of the inner metatarsal bone. It will be remembered that in the metatarso-phalangeal joint of the big toe there is lateral as well as antero-posterior movement, so the position of the first phalanx is necessarily not fixed. The lateral range of movement of the big toe is limited to about twenty degrees, that is, between the one extreme and the other. In spite of this degree of lateral mobility, it is generally easy to observe that the first phalanx

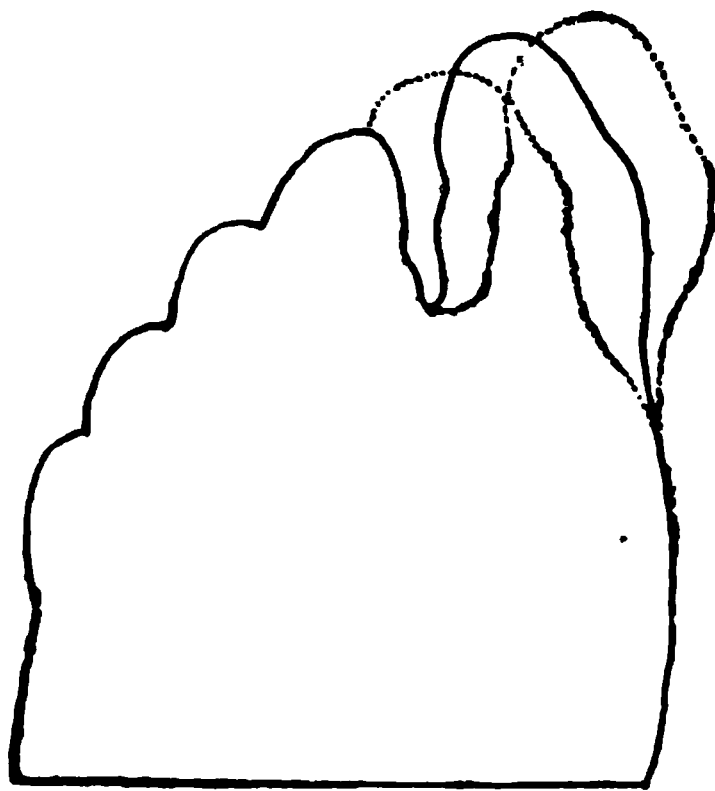


FIG. 3.—Outline of anterior part of foot and toes, showing the range of movement in a horizontal plane of the big toe—(half nat. size).

does usually deviate outwards from the line of the inner margin of the foot to which the inner metatarsal bone is set at an angle. In some examples this deviation is so small as to be difficult of determination, whereas in others it may be as great as twenty degrees, the average being about ten. Between the two phalanges the joint surfaces are shaped in such a way as to prevent any movement except that in an antero-posterior plane, lateral motion being absent. The terminal phalanx invariably deviates outwards, and its axis may diverge as much as twenty degrees from that of the first phalanx.

We find, then, that in a normal big toe the first phalanx deviates outwards from the inner line of the foot, and even more from the axial line of its corresponding metatarsal bone, and

that the terminal also turns outwards from the central line of the first phalanx. These three bones, which lie end to end, are indeed set in a gentle curve with its convexity inwards towards the middle line of the body. The above characteristics in the form and outline of the phalanges and the position they occupy

FIG. 4.—A horizontal section of left foot of foetus born at full term, showing that the proximal phalanx of the big toe is deviated 4° in an outward direction from the long axis of its corresponding metatarsal, and that the terminal turns 12° outwards from the axis of the proximal phalanx—(nat. size).

in respect to one another in the adult are present in the foetus at and even before birth, that is, prior to a time when any external influence whatsoever can be brought to bear on deforming this digit. For in a child born at full term the asymmetry of the phalanges is unmistakable; the deviation in the axis of the first phalanx from that of the innermost metatarsal is often small, but the central line of the terminal turns well outwards from that of the first phalanx.

Accordingly we find in the first pedal digit of the newly-born precisely the same characteristics as those observed in the big toe of the adult, there being perhaps a little less deviation from one another in the central lines of the several bones in the child than in the grown-up, which resolves itself to a difference in degree and not in kind.

It may be of interest to give here some measurements of the degree of deviation of the first segment of the big toe from the inner line of the foot as determined by me in a few specimens of casts of ancient Greek sculpture which I had access to in the Archæological Museum of the University.

(117) 1. Athlete pouring oil into his hand,	.	.	right foot	10°
(271) 2. Wounded Amazon. Pheidias,	.	.	left „	16°
(280) 3. Athlete carrying spear. Doryphoros,	.	.	right „	8°
(291) 4. Young athlete. Idolino,	.	.	left „	20°
(384) 5.	right „	0°
(112) 6. Olympia marble girl starting in a foot race,	.	.	left „	10°
(118) 7. Diskobolus,	.	.	right „	12°
(110B) 8. Charioteer of Delphi,	.	.	left „	8°
Average 10·5°.				

These few measurements suffice to show that the position of the big toe in the feet of the ancient Greeks, as represented by the best sculptors the world has ever seen, is similar to that occupied by the toe in the foot of the modern Britisher, that is to say, it lies more or less midway between the extremes in its lateral range of movement.

In the Museum of Anatomy in the University there are skeletons of the ancient British, of Negroes, of Australian Bushmen and others, one and all of which show, and without any doubt, the distinctive features of the big toe which have been pointed out above.

Owing to the kindness of Professor Macalister I am able to show you that these characteristics of the big toe are well exemplified in the feet of ancient Egyptians, for in them also the phalanges are asymmetrical, and they deviate in the same direction, namely, outwards from the first metatarsal bone and from one another, just as they do in us who live at the present time.

Accordingly, in reviewing our data we may say that in the newly-born child, in the adult, in the savage as well as in civilised man known to us the big toe presents the same characteristics. It is asymmetrical, it is gently curved in its long axis with the convexity inwards towards the opposite foot, and it is directed outwards more or less from the inner line of the foot as well as from the line of the innermost metatarsal bone.

From the above it is clear the big toe does not possess a straight axis in any position; for even if the first phalanx be in a line with that of its metatarsal, the terminal phalanx deviates outwards, even it may be to as much as 20° .



FIG. 5.—View from above of anterior portion of left foot of an ancient Egyptian, showing the inclination outwards of the big toe—(half nat. size).

The results of the above observations are opposed to the views of Professor Meyer, from whose pamphlet the following quotation is taken.

“The great toe plays by far the most important part in walking; because when the foot is raised from the ground with the intention of throwing it forwards, we first raise the heel, then rest for a second on the great toe, and in lifting this from the ground the point of it receives a pressure which impels the body forwards. Thus, in raising the foot, the whole of the sole is gradually as it were ‘unrolled’ up to the point of the great

toe, which again receives an impetus by contact with the ground. The great toe ought therefore to have such a position as will admit of its being unrolled in the manner described; that is to say, it must so lie that the line of its axis, when carried backwards, will emerge at the centre of the heel; and this is its position in the healthy foot."¹

FIG. 6.—Reduced half imprint of right foot, taken when standing erect upon both feet.

It has already been shown that the axis of the big toe is not such as to admit of its prolongation backwards in a straight line to emerge at the middle of the heel, for it forms a curved line in the normal first digit, also that this digit usually lies in a position practically midway between that of extreme abduction and full adduction. The axis of the first phalanx would, as a

¹ *How the Shoe Pinches*.—(Trans. by Craig, p. 20.)

rule, if continued backwards, leave the foot just behind the metatarso-phalangeal joint, and if projected backwards, would pass clear, and well to the inner side of the heel. Thus, even the line of the first phalanx does not follow the inner border of the foot. Professor Meyer, from a study of how we walk, conceived that the big toe ought to lie in a definite line in what he regarded as the ideal normal foot, but the data upon which he built up this conception are incorrect, inasmuch as the big toe has a curved and not a straight axis, and that the central line of the first phalanx, except perhaps when the big toe is in a position of extreme abduction from the middle line of the foot, would if projected backwards emerge well to the inner side of, rather than through the centre of the heel.

Sufficient evidence has, it seems to me, been produced to show that Meyer's views with regard to the position of the big toe in the healthy foot can no longer be entertained, but the good work he did in drawing attention to the evils resulting from ill constructed boots and shoes continues to exercise its beneficent influence.

The asymmetry of the big toe and its inclination outwards in the mean position of its lateral range of movement may perhaps be accounted for by a simple mechanical theory which has occurred to me, and which I will endeavour to explain. When we stand, the imprint of the foot shows that the weight of the body is borne upon the heel, outer border of the foot, and anterior part, formed chiefly by the ball of the big toe on the inner side and that of the little and 4th toe on the outer. Thus the weight of the trunk is borne behind on the narrow heel and in front on the broadest part of the sole of the foot, constituted by the anterior end of the metatarsal bones. While in this attitude the toes do not come in contact with the ground. When, however, we stand on one foot, we rest upon the toes as well as upon the sole in order to increase our steadiness, and when we take a step forward we come to rest upon the anterior ends of the metatarsal bones, the whole length of the big toe and the tips of all the smaller toes (see fig. 8). The weight of the trunk in this phase of the act of walking is borne upon a small triangular area, which is formed behind by the anterior portion of the sole, on the inner side by the big toe, and

on the outer by the tips of the other toes. From the imprint (see fig. 8) it is obvious that, leaving out the part borne by the sole, the big toe bears the greatest proportion of the weight of the body, but the other toes take their share, which is

FIG. 7.—Plantar impression of right foot of an adult, showing the inclination outwards of the big toe. The foot was placed fully on the ground and stood on—(half nat. size).

but a small proportion of the whole. The big toe being much larger than any of the others and therefore more capable of bearing weight, is placed in an advantageous position to

receive and to bear the weight of the trunk in the last phase of the act of stepping off, and the nearer it approaches the middle line of the foot the better it can accomplish this work. Accordingly, it would appear that the big toe inclines outwards so as to be in the position, or as near as possible to it, where it can best receive and bear the weight of the trunk while the person is walking or standing on 'tiptoe.'

Doubtless, the same purpose could be attained by greater growth in one of the middle toes, but as they are diminutive in size, there must be some reason why the big toe has usurped in such a large measure the function of the others. Without entering into a discussion upon this subject, it might suffice for our present purpose to point out that the big toe serves, in

FIG. 8.—Reduced half imprint of right foot, taken when standing on 'tiptoe.'

addition to receiving and bearing the weight of the body in walking, to give the last push in impelling the body forwards, and it does this from its inner border, because the foot in adults is turned more or less outwards during the act of walking.

It would therefore appear that the asymmetry of the segments of the big toe and its inclination outwards clearly serve two purposes, namely, (1) to receive and to bear the weight of the body in walking, and (2) to give the last push forwards. The special construction it possesses can, it seems to me, be fully explained by the mechanical theory put forward above.

I am aware that both Prof. Meyer and Mr T. Ellis consider that

the man who walks as he should turns his foot inwards, but this is certainly not the way in which he does walk; and were he to walk thus, he would at once lose that firm and stable carriage he now possesses. The infant tends to walk with its foot turned inwards so long as it is necessary for it to spread out its lower limbs to gain stability, but as the limbs are adducted to their natural and upright state the turned-in foot gains the position (turned outwards) it occupies in the adult.

ON TWO CASES OF DENTAL ANOMALY. By O. CHARNOCK
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College, Edinburgh.*

ALTHOUGH it is not claimed that the two cases of supernumerary teeth which form the subject of the present paper will throw any dazzling light upon any of the many problems with which odontologists concern themselves, it is nevertheless considered that, if only on account of their rarity, they should be recorded. They both occur in ungulate animals, the one in the horse, the other in the calf.

It is apparently somewhat rarely the case that the members of the Equidæ are provided with supernumerary teeth elsewhere than in the incisor region, only very few instances of additional cheek-teeth being met with in the literature. Magitot (1), Bateson (2), and Hensel (3) have mentioned examples of supernumerary molars in the horse, but they mostly differ in some respect or other from that to be here described.

At the beginning of the present session, my colleague Professor Dunstan placed in my hands the skull of a horse minus the mandible. The specimen, which had apparently been part of the skeleton of a mare of some six or seven years, had been rescued from the bone-heap of a horse-slaughterer's yard. It was in a good state of preservation, and contained all the teeth with the exception of four of the incisors, which, judging from the alveoli, had not presented any points of importance. Obtained, as the specimen was, from a promiscuous collection of bones, the mandible could not be found.

An examination of the teeth reveals the following conditions. Four incisors are missing, as just stated. The third incisor is present on both sides, and possesses the normal characters of such a tooth. The canines are absent, this being a sexual character, which leads one to say that the skull is that of a female. So far, therefore, the dentition is normal. The cheek-teeth, however, at once arrest attention, as there are seven of them on each side of the skull. The first five are well-formed; possibly slightly larger than might have been expected in a

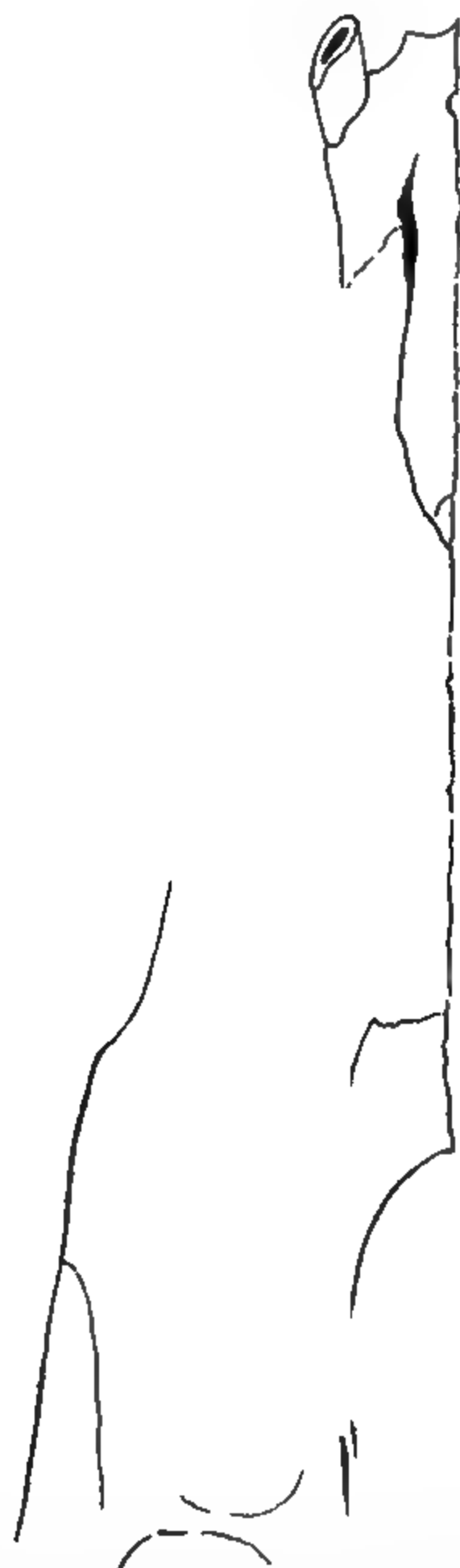


FIG. 1.—Right half of the dental series of a horse with seven cheek-teeth. The unshaded part of the seventh tooth indicates the area which was worn down obliquely.

skull of such dimensions, and show the pattern on their wearing surface which is customarily produced by the intricate folding of the enamel so characteristic of the teeth of the horse tribe. (Compare the pattern on the third cheek-tooth of fig. 1 with that shown in fig. 2, A.) The sixth tooth (m^3) is as large as a normal fifth tooth, and has the same form and pattern. The seventh tooth is large and well formed, having the dimensions and shape of a normal m^3 . A small area along its anterior border has been worn down obliquely, but the rest of



Dentine

Cement

B

FIG. 2.—A. Typical pattern, produced by wear, on the crown of the right pm^3 of the horse.

B. Typical pattern on the right m^3 —(nat. size).

the crown projects above the general level, and shows the elevations and depressions found on an ordinary unworn last molar tooth. There can be no doubt that, had the whole crown been subjected to wear, the same sort of pattern as that usually found on the last molar would have been produced. (Compare fig. 1 with fig. 2, B.) The supernumerary teeth are equally well developed on the two sides of the skull.

One naturally wishes to know the condition of the lower teeth. As this is impossible from actual observation, a conclusion must be arrived at from inference. There seems to be

no reason to suppose that the lower teeth presented any abnormality whatever, and this impression is readily obtained from an examination of the worn surfaces of the upper teeth. Under normal circumstances, the upper and lower molars and premolars of the horse bite against each other as shown in the accompanying diagram (fig. 3), and, as a result of friction, certain regular inequalities are produced. In the specimen we are considering, these inequalities are present in the orthodox form in the premolars and the first three molars. The obliquely worn part of the seventh tooth can be accounted for without supposing that there has been a small opposed lower tooth. The last molar always extends a little farther back in the lower than in the upper jaw (fig. 3), and therefore we may assume that the sixth lower tooth would impinge upon the anterior part of the seventh upper tooth sufficiently to produce the small worn area in question. Further, accessory teeth in the lower jaw are rare, and in none of the recorded cases have they been present on both sides.

In reference to the significance of this supernumerary tooth, two questions naturally suggest themselves. In the first place, is it possible that here is an instance of unusually large development and persistence of the normally small and ephemeral first premolar? As is well known, the first premolar of the horse is small and conical, and—appearing at an early age—usually disappears before the animal has reached what may be described as its mature condition. This small tooth is hardly ever—possibly we may say never—present in the lower jaw, and therefore, when found in the upper jaw, has no tooth immediately below it. If, then, its development were to go on to the production of a tooth as large as the normal second premolar, it seems not unreasonable to expect that the upper series of teeth would extend farther forwards than the lower, or else that the normal relationship of upper and lower teeth would be disturbed. The appearance of the worn surfaces of the upper teeth shows that neither the one nor the other of these conditions obtained. Then again, if the normally small first premolar were to increase in size, we should hardly look for it to attain to the full size of a second tooth with foldings of enamel so complicated as to give us the normal pattern on

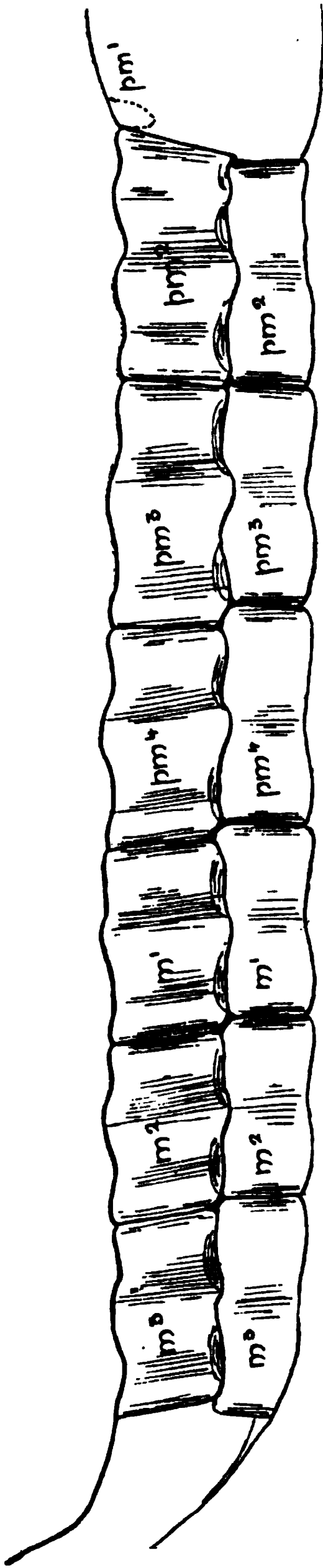


FIG. 3.—Diagram showing how the upper and lower premolars and molars of the horse bite against each other.

wear. Lastly, when the rudimentary first premolar disappears, its alveolus speedily fills up with bone, and the only evidence of its previous existence is a slight irregularity of surface over the spot formerly occupied by it. The skull with the seven cheek-teeth had belonged, as already stated, to an animal of six or seven years of age, an age at which the first premolar has usually disappeared and its alveolus has become obliterated. An examination of the bone in front of the first cheek-tooth shows a faint inequality, which no doubt marks the former site of the small alveolus. We may therefore, without much hesitation, answer the first question in the negative.

The second question which presents itself is this: If it is not a case of reversion towards the *Hipparion* dentition, can it possibly be reversion towards some ancestral form in which there were normally four molars?

This is not at all likely, for ancestors with four molars must be very far removed from the modern horse, and reversion does not take place towards forms palæontologically remote.

The most feasible conclusion at which one can arrive is, that the supernumerary tooth is merely a variation, resulting from a more than usually extensive backward prolongation of the dental lamina, and the formation from it of one dental germ in excess of the normal number. The fact that the sixth tooth has the form of an ordinary penultimate tooth offers no obstacle to the assumption that the extra dental germ was developed at the most posterior part of the dental lamina, and not at some more anterior point; for Bateson (4) has shown that in those cases where, in consequence of the presence of an additional tooth, the normal ultimate tooth becomes the penultimate, this penultimate is found to be larger and better developed than the normal ultimate tooth in an animal of corresponding size.

The literature contains only a very few cases similar to the one described above. Magitot (1) describes and figures the earliest recorded case of which I can obtain any information. Here, the additional tooth is only present on the left side of the upper jaw. Hensel (3) remarks the rarity of an increase or decrease in the number of molars in Herbivora, and expresses the opinion that, on theoretic grounds, such variation should occur more frequently in the lower than in the upper jaw. He

exemplifies this opinion by stating that he has a horse's skull with *m* 4 on each side of the lower jaw; the teeth being fairly well developed, but hardly projecting beyond the level of the bone. He admits that the rule is not always followed, and mentions that his colleague Dr Crampe has in his collection a skull with *m* 4 on both sides of the upper and on the left side of the lower jaw.

The only other case having direct bearing upon the present anomaly, to which I can find reference, is mentioned by Bateson (2), who states that in the skeleton of a thoroughbred Spanish she-ass, in the Museum of the Royal College of Surgeons, London, there is a large supernumerary molar tooth on each side in series in the upper jaw, and a similar tooth in the left lower jaw. Wishing to learn more precise details regarding this case, which has never been fully described or figured, I wrote to Professor C. Stewart, Curator of the Royal College of Surgeons Museum, and he very kindly gave me the following particulars, for which I here desire to express my thanks:—"The left extra molar in the upper jaw has its crown obliquely worn down, its posterior border being below the general level of the other teeth. The right extra tooth is only worn down in front. Both teeth are of the size of the last molar in an ordinary ass. In the lower jaw the extra molar looks like a last molar; the one in front of it being somewhat more square than normal." The conditions here described are of interest, as showing what the teeth in my case would have been like had there been supernumerary teeth in the lower jaw.

The second case of abnormal teeth is one of even greater interest than that described in the preceding paragraphs; for, so far as I can discover, it is absolutely unique of its kind. The teeth, two in number, were found in the premaxillary region of a calf. It is rather unfortunate that the face of the animal was deformed in a marked degree; but the deformity, though unfortunate, does not remove anything from the value of the case.

The head and neck of a full-grown and naturally-born calf was handed to me as a teratological specimen. Apart from the head, the animal had been well developed, and of somewhat more than average size. Examination of the head showed

that it was a well marked example of anencephaly. The

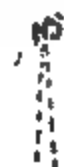


FIG. 4.—Face of the anencephalic calf, viewed from the front. Drawn from a photograph.
1, fronto-nasal process; 2, upper cheek-teeth; 3, hard palate, turned upwards as a result of the extensive deformity of the upper part of the face.

cranium was very defective, and the brain was only represented by a medulla and pons, and a short tapering continuation in place of the crura cerebri. There was no cerebrum, and only a very doubtful apology for a cerebellum. The face had also fallen very far short of full development. Some idea of the



FIG. 5.—Fronto-nasal process of the calf—(nat. size). 1, the part of the tooth which was projecting beyond the gum ; A B, line of section shown in fig. 6.

appearance presented by the face may be gained from the accompanying sketch (fig. 4). Obviously the only processes which had met and fused were the mandibular, the growth of the rest being very abortive.

Projecting from what should have been the region of the

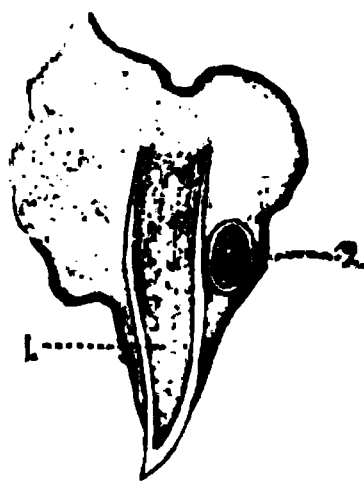


FIG. 6.—Longitudinal section through one of the teeth of the calf. 1, tooth cut longitudinally, showing pulp-cavity ; 2, transverse section through the root of the other tooth—(nat. size).

forehead was a short fronto-nasal process (fig. 4, 1 ; and fig. 5). From the most anterior part of this process the tips of two teeth projected through the mucous membrane (fig. 5, 1). The process, which contained a small quantity of bone, was removed and decalcified, and sections were made in the long axis of one of the teeth. The sections (fig. 6) showed that the teeth were

very well developed, had definite pulp-cavities, and were arranged with their roots crossing each other at almost a right angle. It should be here stated that these teeth had not the form of the lower incisors and canines of a calf, but bore a resemblance to the incisors or canines of a camel.

The lower incisors, canines, and cheek-teeth, and the cheek-teeth in the upper jaw, were quite normally developed, and did not differ in any important detail from the teeth usually found in a new-born calf.

The circumstance that premaxillary teeth are absent in all, and that superior canines are present in some only of the Pecora, or true ruminants, has led several observers to inquire into the embryological history of the premaxillary region of the more common ruminants. Apparently the first inquiry was conducted by Goodsir (5), who came to the conclusion that dental "germs presented themselves (in the embryos of the cow and sheep) under the form of slight dimples in the primitive groove, and that, after the closure of the latter, they remain for a short time as opaque nodules imbedded in the gum, in the course of the line of adhesion." This statement, made in 1839, obtained universal credence until 1873, when Pietkewickz (6) made a directly negative assertion. He said that in an extensive series of embryos of the cow and sheep, "*pris depuis le moment le plus reculé de la vie embryonnaire jusqu'à une longueur de 30 centimètres, non seulement je n'ai jamais constaté la présence de follicules, mais je n'ai même jamais trouvé trace de la lame épithéliale.*" Legros and Magitot (7), in their observations on the development of the teeth of mammals, do not make any assertion on their own account, but merely quote Pietkewickz.

The results of investigations by Piana (8) led him to the conclusion that the dental lamina of the upper jaw extends as far forwards as the region where the lateral incisors should develop, and that enamel germs of canine teeth exist at a certain stage of development, but soon disappear. Pouchet and Chabry (9) allow that there is a dental lamina in the sheep, but deny that its development is at all extensive. They say, "*Dans la région qui correspond verticalement à la deuxième incisive inférieure, sur un embryon mesurant un peu moins de*

5 centimètres, la lame se présente comme un petit prolongement aplati et vertical du bord profond du mur plongeant. . . . Plus en avant la lame se confond insensiblement avec la crête du mur sans qu'il soit possible de lui assigner une limite antérieure. Ainsi, non seulement la région incisive des ruminants, ne présente aucun vestige de dents, contrairement à ce qu'on avait cru à une certaine époque mais elle ne possède pas même de lame dentaire différenciée, dans toute son étendue." The latest contribution to the question comes from the pen of Miss Florence Mayo (10), who, having examined embryos of the sheep, arrives at the following conclusions:—“(1) That in the embryo sheep at a certain stage of development, the dental lamina exists throughout the canine and incisor regions of the upper jaw. Its anterior portion, which is the *last* to develop and the first to abort, does not attain so prominent a condition as its lateral portion. After advancing in development for a time, it retrogrades and finally disappears. (2) That in the canine region the dental lamina gives rise to an enamel germ which never reaches a stage of functional activity; for neither are its central cells transformed into a stellate reticulum, nor do those of its malpighian layer ever produce enamel, and in later stages both disappear.”

Such is the evidence; and from it we may judge that there is at least an attempt at tooth-formation in the canine and incisor region of the upper jaw of, at any rate, some ruminants. Both comparative anatomy and embryology point to the possibility of the reappearance of these lost teeth, and indicate that the canines are more likely to develop than the incisors. It is a great pity that the calf in which the teeth described in this paper were present, was so far deformed as to make it somewhat doubtful whether the abnormal structures were canines or incisors. But their definite location in a premaxillary bone, or bones, albeit rudimentary, makes one incline to the supposition that they were incisors.

It seems well that the above two cases should be described together, inasmuch as they illustrate two distinct varieties of dental anomaly. In the case of the horse the variation was not in any way related to ancestry, but was merely an instance

of multiplication of serial organs in the individual. The case of the calf, on the other hand, may reasonably be taken as an instance of reversion towards an ancestor provided with a fuller complement of teeth than is present in the modern Bovidæ.

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- (9) POUCHET, G., and CHABRY, L., "Contribution a l'odontologie des Mammifères," *Journ. de l'Anat. et de la Phys.*, T. xx., 1884, p. 149.
- (10) MAYO, FLORENCE, "The superior incisors and canines of sheep," *Bull. Mus. Comp. Zool. Harvard*, vol. xiii. No. 9, 1888, p. 247.

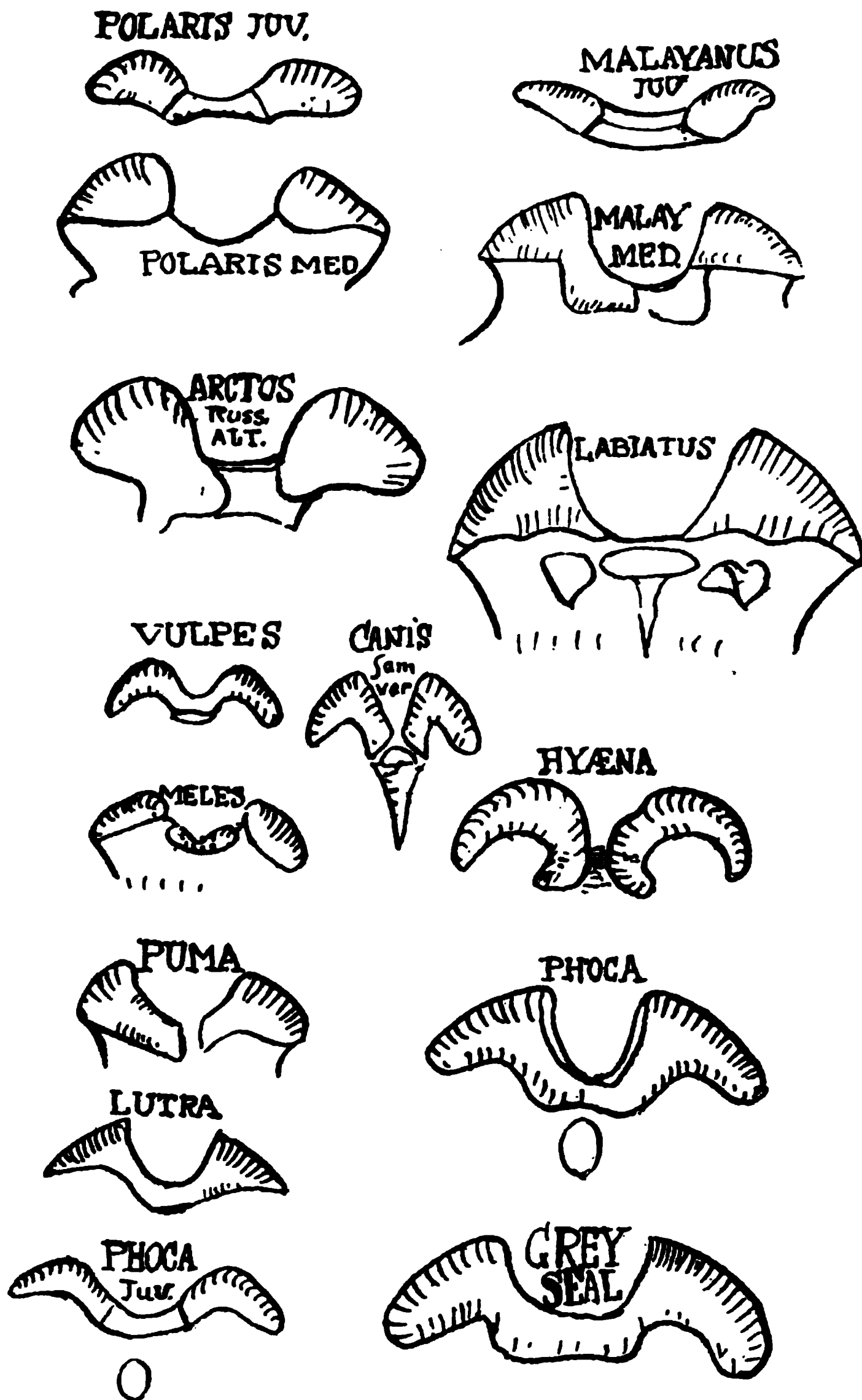
A NOTE ON THE OCCIPITO-ATLOID ARTICULATION
IN SOME ARCTOIDS. By R. J. ANDERSON, M.D.,
Queen's College, Galway.

PROFESSOR OWEN mentions that the articular surfaces of the condyles in the otter (*Intra vulgaris*) are continued across the middle line. In the skull of a badger (*Meles taxus*) in this museum a like condition prevails; in a second skull, which seems older, the mesial articular surface is not well marked.

It will be remembered that Dr Carl Strecker published and supplemented the work on occipital condyles which Professor Reichert left unfinished at his death. He says, about *Ursus Americanus* and *U. (Melursus) labiatus*:—"U. Americanus und U. labiatus haben beide walzenförmig, mehr oder weniger stark gekrümmte Condylen. Ihre craniopetalen Flächen stossen medial sich wenden zusammen, so dass bei U. labiatus am ventralen Rande des Foramen magnum eine schmale herzförmige Gelenkfläche entsteht (deren Spitze craniopetal sich auf dem os basilare, erstreckt, deren Basis jedoch durch das Foramen magnum concav wird, was bei U. Americanus zwar auch der Fall ist) wo jedoch auch das craniopetale vereinte Flächenstück concav begrenzt ist, so dass die mediale Verbindungsfläche schmetterlingsförmig wird." The central articular basilar surface of *labiatus* seems to consist of a mesial part and two lateral, which are separated from the correct condylar articular portions by slight grooves. The lateral surfaces are also separated by grooves from the mesial surface. *Americanus* has the condyles just one-eighth of an inch apart at the anterior part of the foramen magnum. The lateral prolongations are like those of *labiatus*, but there seems not to have been any mesial portion. It will be remembered that Gray was struck by the varieties to be met with in Bears, referable, as it seemed, to the same species.

Taking an *Arctos*, which was stated to be Russian, the head of this bear was disarticulated by myself, so that the natural condition was observed. The specimen seemed old. The transverse diameter of the condyles right across the foramen was

2½ inches from out to out. The greatest breadth of each



condyle $\frac{3}{4}$ inch. The distance between the condyles behind is 1 inch. The articular surface is convex, narrow towards the

front and notched on each side externally. Behind, the articular surface looks downwards, outwards and backwards; anteriorly, where it tapers, the surface looks forwards, and is continued across the middle line to join the prolongation of the opposite condylar articular surface. A slight notch at the right side, filled with synovial tissue, marks the appropriate limit of the condyle. One is reminded here of the condition of the synovial process of the olecranon in Man. The atlas may have, of course, extended its bed or range. The notch on the right side is not repeated on the left side. The anterior articular surface is $\frac{3}{16}$ th inch in breadth. The atlas presents corresponding articular surfaces above; these taper on each side anteriorly, and are just separated from a narrow synovial part behind, which reaches from side to side for $\frac{3}{8}$ ths of an inch. The axial articular surfaces below taper and touch anteriorly.

Compared with the skull of a lioness of which the sutures still remain, it is to be noticed that whilst the condyles in the latter are separated for $\frac{1}{8}$ th inch, each articular surface is continued into the basilar process, and this basilar portion is $\frac{1}{2}$ inch from side to side by $\frac{1}{8}$ th inch. The articular surface is grooved on each side by transverse continuous furrows. It may be mentioned that in several heavy-headed animals there is an extension forwards, *e.g.*, a buffalo has a forward extension. The extension is hollowed in two tapers. A groove runs in front of a median prominence in a kangaroo (*Bennettii*), whilst in an elephant the condyles are much separated ($\frac{1}{2}$ inch), but occupy a portion of the basilar part.

Professor Owen referred to the prominent ridge joining the condyles in front of the foramen magnum in *Ursus Polaris*. It will be remembered that the condyles are widely separate in the adult in front. In the young there may, it seems, be a different arrangement. In a specimen under notice the condyles taper internally, and are continued in front of the foramen magnum. The line of junction of the basilar articular surface with the lateral is clearly shown by the junction of the condylar with the basilar portion. The basilar articular surface is much narrower internally than externally.

The adult Malay bear shows a well marked prolongation of the articular surfaces across the middle line. A young Malay-

anus, with a skull 6 inches long, has the condyles united by an articular surface in front of the foramen magnum. A groove separates the condyles in *Thibetanus*, and in *ornatus* also. The condylar articular surfaces are separate. In this latter curious American form, the condyles anteriorly run flush with a central platform on the basilar process, which may have had a bursal prolongation of the articulations attached to it. It will be remembered that De Blainville pointed out a similarity in general features in this skull to *Malayanus*. It resembles in some respects *labiatus*. The mesial portion of the basilar surface is not unlike that in *labiatus*.

Meckel says, in speaking of the seals, "Die Gelenkköpfe sind breit"; in seals and walruses, "und stossen in der Mittel durch eine schmale, vordere Verlängerung fast zusammen." In an adult phoca which I have before me there is a strip of cartilage connecting the condyles; the surface is mesially convex, but externally concave. In a young seal the condyles are joined by a narrow articular surface; this latter is $\frac{5}{8}$ th inch broad and $\frac{1}{8}$ th inch wide at the middle, and $\frac{3}{16}$ th inch wide at each end. The continuous mesial surface of *Halichoerus* is also worth noting. There is here a small crescentic piece of bone which projects backwards from the anterior margin of the foramen magnum, forming a special platform, as if an inner table existed whose margin reached outward to the condylar foramina. The basilar process is much hollowed in the middle line above, and is not perforated, although greatly thinned. I have to add that the tailing out of the condyles in *Hyæna*, which leads to an X-shaped appearance, seems worth mentioning in this connection. Meckel took care to mention the direction of the condylar axes, and it is possible that conditions such as exist in *Thalassarctos* may prevail, viz., an articular junction in youth, which is afterwards dispensed with, temporarily or permanently; secondly, two separate condyles at first may be supplemented by a bursal or permanent third articular surface, or the condyles may get an extension; lastly, the basilar strip of the otter and seal may continue throughout life.

TWO RARE VERTEBRAL ANOMALIES. By E. BARCLAY SMITH, M.D., *Senior Demonstrator of Anatomy, University of Cambridge.*

IN the *Anatomischer Anzeiger* of December 1901, Szalowski of St Petersburg, in a paper on Vertebral Anomalies, describes what he terms foramina transversaria in the 5th lumbar and 1st sacral vertebræ, or, if the ventral limiting element in either case is to be regarded as costal, costo-transverse foramina would be a more suggestive title.

Both lumbar and sacral conditions were probably previously

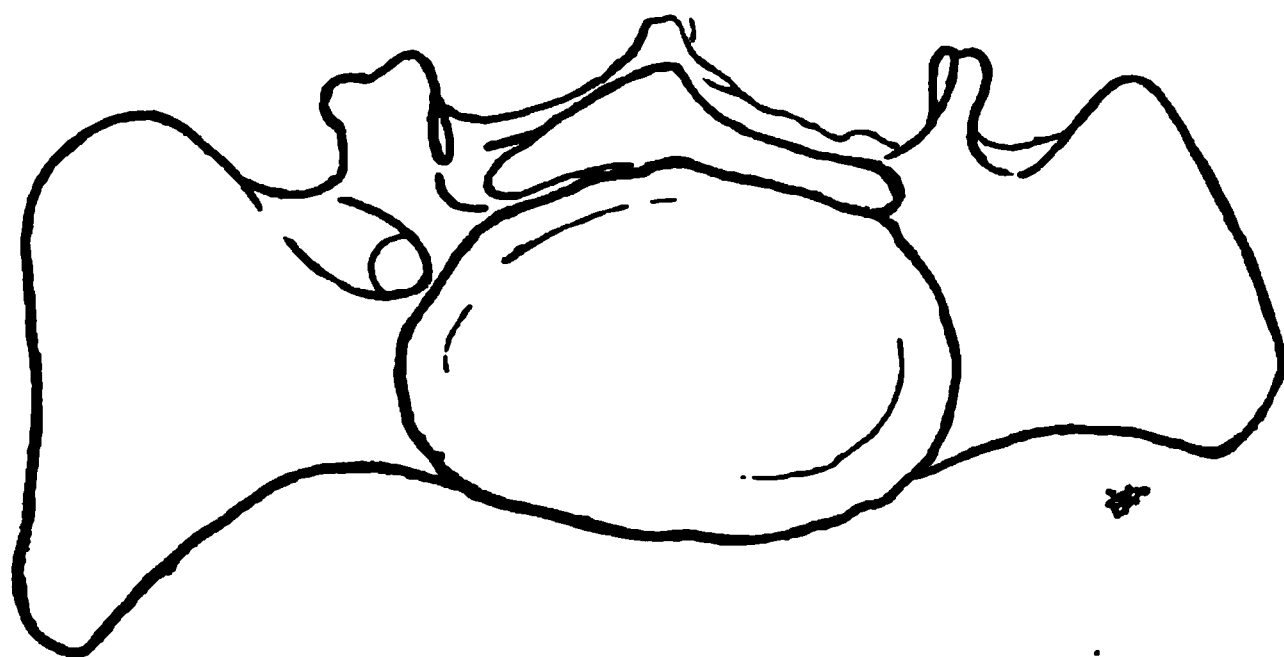


FIG. 1.

unrecorded, but Dwight in February 1902 published an account in the same journal of a precisely similar condition in a lumbar vertebra, while the sacral condition has its complement in the case under present notice.

As may be seen from fig. 1, the pedicle of the 1st sacral segment is differentiated from the lateral mass on the right side, and thus gives rise to a rounded hole leading downwards into a space common to the anterior and posterior sacral foramina between the first two sacral segments. There are some remarkable similarities to the case described by Szalowski, *e.g.*, the anterior foramina between the first two sacral segments are of unequal size, that on the right or anomalous side being 18 mm. in vertical diameter, while the left was only 15 mm. These figures present a striking likeness to Szalowski's case, where the first anterior

sacral foramen was 17 mm. high on the left or anomalous side, and 14 mm. high on the right; as in his case, the corresponding posterior sacral foramina do not exhibit any appreciable discrepancies. In the case under notice the first sacral segment exhibits marked asymmetry. The lateral mass, if viewed from above, is markedly larger on the right side, and concomitant with this is a more extensive and more vertically elongated auricular surface. The sacral canal is more capacious on the right side, and the spinous process is displaced rightwards of the median sagittal axis of the centrum. There is great disproportion between the mammillary processes, that on the right side being far the larger. The asymmetry does not appreciably affect the lower sacral segments, except so far as the vertical elongation of the right auricular surface is concerned.

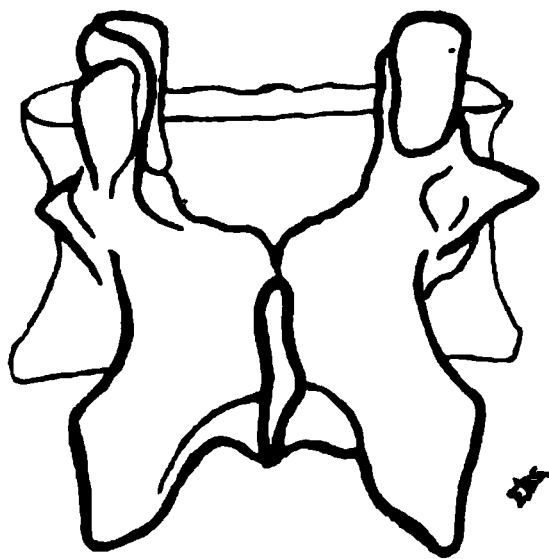


FIG. 2.

Fig. 2 presents a dorsal view of what is very rare as an example of vertebral asymmetry. It is taken from a vertebra which, from the contour of the spinous process, from the presence and situation of the costal facets, is probably a 12th thoracic. The lower articular processes present the usual lumbar characteristics. The upper articular processes, however, present a remarkable contrast. The right is of the normal thoracic type, with a flattened, dorsally directed articular surface, and surmounting the stunted tuberculated process so characteristic of the 12th thoracic. The left is typically lumbar, presenting a deeply concave articular surface, directed mesially, and with both mammillary and accessory processes well marked. On both sides the pedicle exhibited a vertically disposed vascular canal. This is a feature more frequently found in the twelfth thoracic than in

any other vertebra of the same series, and concerning which I hope to make a further communication. It is interesting to note that the 11th thoracic must have exhibited reciprocal conditions. As to the causation of such an anomaly it is impossible to guess, or to hazard a suggestion as to the kind of movement which could take place between such a vertebra and its reciprocal.

Since the above was written, four other examples of this anomalous condition of the articular surfaces have been found, in all of which the flat facet is on the right side. .

ON THE NATURAL PRESERVATION OF THE BRAIN IN
THE ANCIENT EGYPTIANS. By G. ELLIOT SMITH,
*Fellow of St John's College, Cambridge; Professor of Anatomy,
Egyptian Government School of Medicine, Cairo.* (PLATE
XIV.)

ALMOST every archæologist who has excavated in any of the innumerable cemeteries with which Egypt is so thickly studded is aware of the fact that the brain is preserved in the crania of a very large proportion of those bodies (of every period) which have *not* been "mummified" by artificial conservative processes.

Anatomists and anthropologists seem to be not only ignorant of this fact, but even deny the possibility of its occurrence. The scanty literature relating to this subject has recently been fully discussed in an interesting memoir¹ dealing with the brain of an Indian of Ohio which had become desiccated and preserved by natural agencies. The author seems to imagine that a similar phenomenon has rarely or never occurred in Egypt. He says, in fact, that he has been able to find only "a single record of the undoubted finding of a brain," and adds: "I would not be understood as saying that this is the only case of the kind recorded, but it is the only one I have been able to find. In view of the fact that it is estimated that about four hundred millions of persons were embalmed in the 4700 years [*sic*!] in which the Egyptians practised embalming, it is curious, to say the least, that there would appear to be but one such case recorded.

"The most interesting question is, how this brain, an organ so very perishable under ordinary post-mortem conditions, was preserved. The conditions in this case must therefore have been quite extraordinary."²

¹ D. S. Lamb, "Mummification, especially of the Brain," *American Anthropologist* (N.S.), vol. 3, April-June 1901, pp. 294-307.

The title is somewhat unhappy when it is remembered that it is in these cases to which the term "mummification" is especially applicable that the brain is rarely or never found, because it is carefully removed through the broken ethmoid.

² *Op. cit.*, p. 298.

Elsewhere in the same memoir he refers to Fouquet's remarks concerning the finding of "resinous material" in crania from El Amrah, in which the ethmoid bone was intact, and also to Virchow's statement that it was "an open question whether the masses . . . are or are not brain which has dried and become changed in some thousands of years" (p. 296).¹ It is also stated that "Virchow and other continental authorities" had stated "that they had never met with or heard of a human brain having been preserved by natural agencies, and seemed to doubt the genuineness of the specimen" (p. 305).

In order to settle the question as to the nature of the masses found in the crania, elaborate chemical tests have been made by Salkowski; but even after this, "Virchow was moved to question whether the material was actually brain, or merely embalming material" (*op. cit.*, p. 297).

These quotations will have made it clear that the nature of the intracranial material found in most Egyptian skulls is not yet admitted by anthropologists.

The question is of some archæological importance, because the supposed "resinous" nature of the material has been considered as decisive evidence in favour of the belief in the practice of embalming in the most archaic periods of Egyptian history.

My attention was first called to this subject by my friend Dr W. H. R. Rivers, who told me that he had seen desiccated brains in many of the broken skulls excavated by Mr Randall-Maciver and the late Mr Anthony Wilkin at El Amrah in Upper Egypt. At his request Mr Randall-Maciver sent me some specimens of this material obtained from crania of the predynastic, protodynastic, XII. and XVIII. dynastic periods, and also permitted me to examine some skeletons *in situ* at El Amrah. Since then I have obtained similar intracranial masses in other cemeteries, ranging from the earliest prehistoric times through all periods to recent Coptic. A detailed report on all this material will shortly be published. At present I shall refer only to the specimens from El Amrah.

In the case of most of the intracranial masses it is apparent

¹ Compare *Verhandl. Berlin. Gesellsch. f. Anthropol.*, 1897, p. 134, and elsewhere.

at the merest glance that the material can only be brain. No one who has ever seen a brain would hesitate a moment to acknowledge this fact, which calls for no elaborate chemical or microscopic tests to confirm its accuracy. Moreover, the circumstances under which many of these brains are found in perfectly intact skulls which have never been severed from the rest of the body complete the demonstration that no foreign matter could have been introduced into the cranial cavity. The intracranial masses undoubtedly consist of brain material which must have become dried and preserved by the operation of natural processes.

The brain is preserved in this manner in the vast majority of the bodies in Egyptian cemeteries. I have seen a prehistoric cemetery containing nearly 500 bodies, in every one of which the brain was preserved. And the same phenomenon occurs in bodies of other periods, especially when the corpse has been buried in dry soil and removed from all direct access to the air. The chief factors which seem to determine the state of preservation of the brain are the position and mode of burial of the body.

If a corpse is placed in the sand in a well-drained situation, far above the level of the Nile-flood, the brain will *certainly* be well-preserved, whether the burial took place in predynastic times, during the Old, Middle, or New Empires, or in Christian times.

This alone would be sufficient to show that it must be the operation of purely natural factors rather than the effect of artificial preservative measures which "mummifies" the brain, even if the other circumstances did not clearly demonstrate this fact.

Is this natural desiccation of the brain such an unheard-of phenomenon as Virchow and others would have us believe?

Since I obtained the specimens from El Amrah I have casually noticed (without special search) in the newspaper press references to the finding of similar dried brains in Australia (in the oldest European cemetery in Sydney), in America (in old Indian burials), and even in the damp climate of England (in an old battlefield). Whilst, however, one would not accept mere newspaper reports as scientific evidence, it must be admitted that these are hardly the kind of stories which even the most imaginative journalist would invent

without some element of fact as a basis. And when we know how exceedingly common such brain-masses are in all kinds of Egyptian graves, it would indeed be strange if similar remains did not sometimes occur elsewhere, even though the conditions were not so uniformly favourable to their production as in Egypt.

The brain-masses are exceedingly variable in size, shape, and colour. They may be as much as two-thirds of the original length of the brain, or they may have shrunk to less than half the length. Their shape is adapted to the configuration of the bony walls with which they are in contact. The lower cerebral hemisphere is consequently convex, and its convolutions are flattened, whereas the upper hemisphere is usually concave, and presents prominent rounded convolutions. The masses may be black or dark brown, breaking with a shining fracture, or they may be of a much lighter brown colour, or even a light grey, and present a wood-like texture. The latter variety often have patches of white substance on their surface. In other cases the brain becomes reduced to a dark brown, coffee-like powder. In the case of many of these masses it is possible accurately to determine the course of every sulcus both on the lateral and mesial aspects of the cerebral hemisphere. In such cases we can obtain a fairly complete idea of the appearance of the brain, for we can determine its size and shape, and the positions of many of its sulci, in a cast of the cranial cavity.

In a memoir, which will be published in a short time, I intend to give a full account of the structure of the brain in the predynastic and protodynastic Egyptians.

In order to convey a more adequate idea as to the nature of the material with which we have to deal, I shall now represent the appearance of the left cerebral hemisphere of a brain from a cemetery of the XII.-XV. dynastic period (*i.e.*, about 2000 B.C., according to Erman's *Aegypten*, at El Amrah (near Abydos).

I have removed the cerebellum and the greater part of the brain-stem and the right cerebral hemisphere.

In profile the left cerebral hemisphere has fairly-closely retained its natural shape, as shown by a plaster mould of the cranial cavity. It is 81 mm. long, whereas its original length was 168 mm.

All of the sulci, both on its cranial and mesial aspects, are easily recognisable. The lips of the Sylvian fissure gape to a slight extent, and fully half of the insula Reilii is uncovered (fig. 1). This is not due to the breaking and loss of any part of

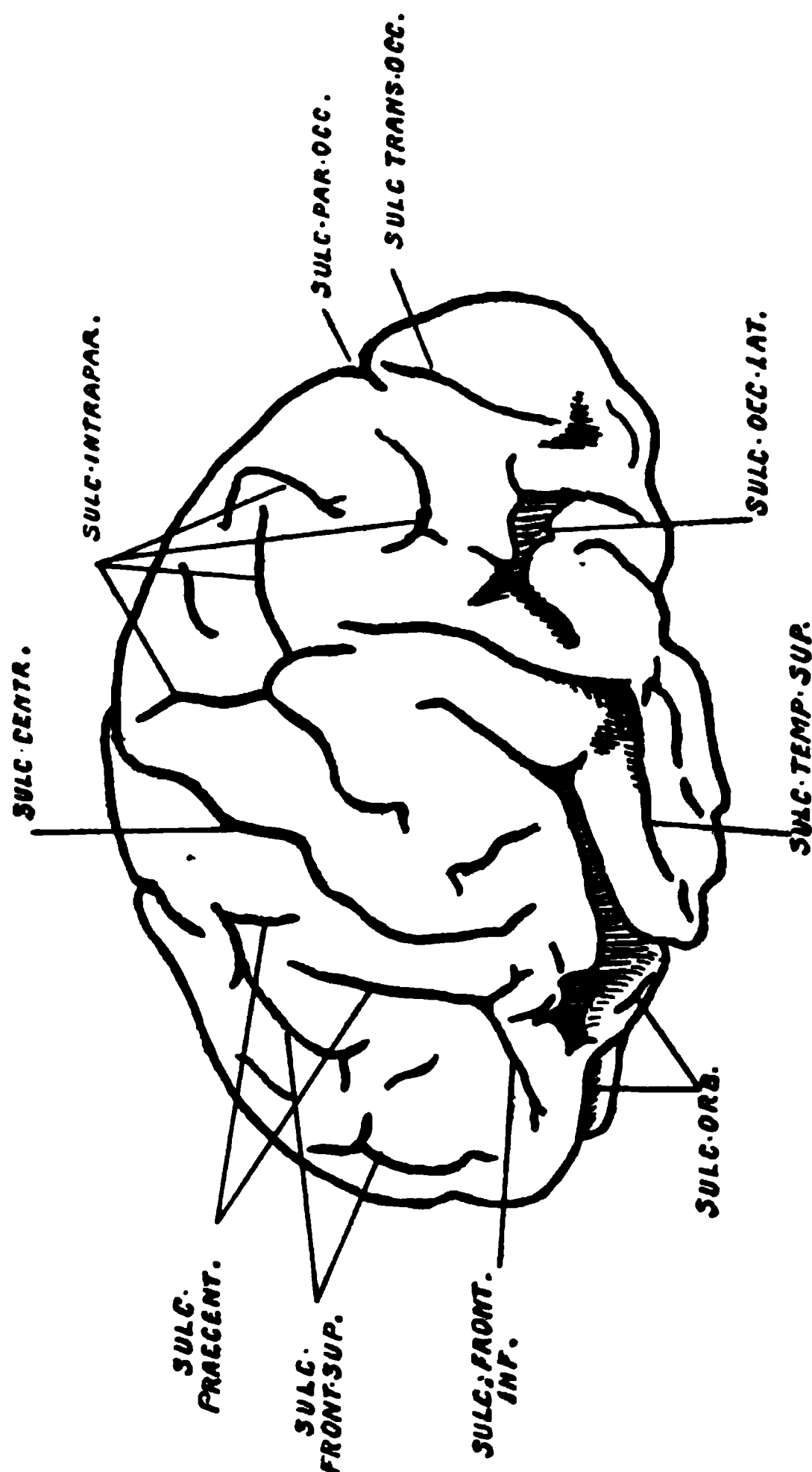


FIG. 1.—The lateral aspect of the left cerebral hemisphere of a brain of the XII. dynastic period—(nat. size).

the opercula. The small ill-developed orbital operculum is quite distinct. It is probable that the insula was partly uncovered, as usually happens in the brain of the modern Fellaheen.

The arrangement of the sulci is clearly shown in the accompanying diagrams, and the actual appearance of the specimen is

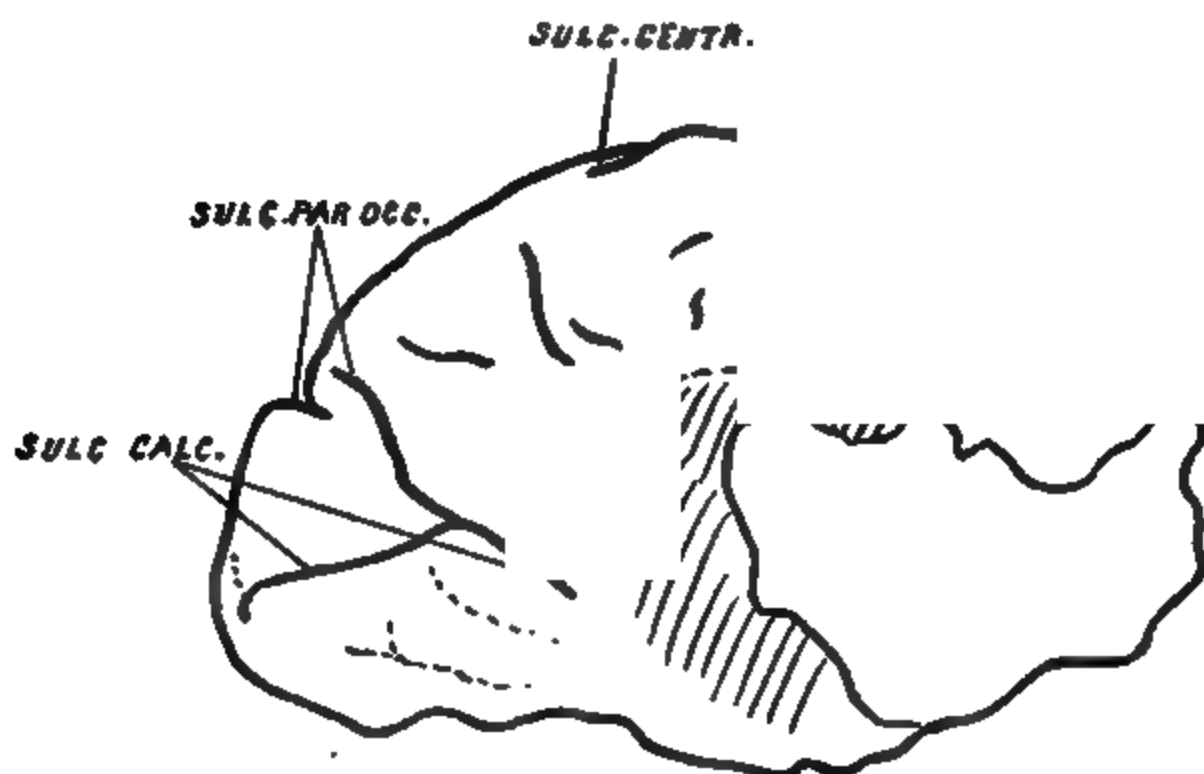


FIG. 2.—Medial aspect of the same hemisphere.

shown in the admirable photographs which have been kindly made for me by Mr Albert M. Lythgoe, of the University of California Egyptological Expedition.

THE PRIMARY SUBDIVISION OF THE MAMMALIAN CEREBELLUM. By G. ELLIOT SMITH, *Fellow of St John's College, Cambridge; Professor of Anatomy, Egyptian Government School of Medicine, Cairo.*

THE researches of Knithan,¹ Stroud,² and the writer³ have clearly demonstrated that the mode of subdivision of the cerebellum usually adopted in treatises on Human Anatomy does not readily lend itself to the needs of Comparative Anatomy.

If the structure of the cerebellum be carefully studied in the whole mammalian group, and those features be eliminated which are not common to the organ in all other mammals, we shall arrive at the fundamental plan which is diagrammatically represented in the accompanying scheme.

The cerebellum is composed of two floccular lobes and a great interfloccular mass which is subdivided by two deep and constant sulci into three azygos lobes—anterior, middle, and posterior respectively. The two fundamental clefts which cross the mesial plane and effect this subdivision of the interfloccular region have been called “fissura prima” and “fissura secunda,” in reference to their relative importance and precocity.

The POSTERIOR LOBE is always a small insignificant mass, which is invariably subdivided into two parts—nodulus and uvula—by a short transverse sulcus. Both of these bodies appear to end suddenly at a short distance from the mesial plane, and to give place to a white band—the posterior medullary velum. But if a series of sagittal sections through the cerebellum of a small mammal be carefully studied, a narrow band of cerebellar cortex will be found extending out-

¹ “Die Entwicklung des Kleinhirns bei Säugethieren,” *Münchener medicinische Abhandlungen*, vii. Reihe, 6. Heft, 1895.

² “The Mammalian Cerebellum,” *Journal of Comparative Neurology*, vol. v., 1895. Also in Wilder's article “Brain,” *Reference Handbook of the Medical Sciences*, 1901, p. 160.

³ “The Brain in the Edentata,” *Transactions of the Linnean Society of London*, vol. vii. part vii., 1899, pp. 360 *et seq.*

ward from each lateral extremity of the posterior lobe to the flocculus.

The FLOCCULAR LOBE is subdivided into two parts in all mammals. There is a small ventro-caudal lobule, representing the flocculus of Human Anatomy, which is linked, on the one hand, to the posterior lobe, and is in contact with the tuberculum acusticum.

The second lobule has been called "paraflocculus" by Stroud. It is placed on the dorsal side of the flocculus. It almost always consists of two limbs—dorsal and ventral—which

and so on

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B

DIAGRAM to represent the fundamental subdivisions of the cerebellum spread out in one plane.

become continuous anteriorly. In the smallest representatives of every mammalian order, the caudal extremities of the dorsal and ventral limbs of the paraflocculus can be clearly seen to be joined to the middle lobe and to the flocculus respectively. The dorsal paraflocculus is linked to that part of the middle lobe which is called the "pyramid" in Human Anatomy, by means of a narrow band of cerebellar cortex, which may be distinguished as the "copula pyramidis."

The paraflocculus is always subdivided by a series of radiating fissures, so that it is converted into an annulated worm-like

band of small folia. This process of subdivision extends to the copula in many mammals. In many representatives of almost every order some part of the paraflocculus—usually, though not always, the caudal extremity of the ventral limb—extends outward as a strongly projecting bunch of folia—the so-called “petrosal lobule”—which becomes lodged in a special fossa in the petrous temporal. In all mammals the floccular lobe is considerably larger than it is in Man and the large Anthropoid Apes; and in some, especially the Sirenia, it becomes relatively enormous. These variations in size depend wholly on the paraflocculus, because the flocculus always remains small.

In the genera *Simia*, *Anthropopithecus*, and *Homo* the paraflocculus dwindles to very diminutive proportions, and forms the insignificant folia of the “flocculi secundarii” of Henle, which can be exposed by drawing the flocculus inward.

The ANTERIOR LOBE is that part which is placed in front of the fissura prima, and includes the regions commonly called Lobus culminis, Lobus centralis, and Lobus lingulæ.

The MIDDLE LOBE is that important area of the cerebellum which is included between the fissuræ prima and secunda. It falls naturally into four parts in almost every mammalian brain. These parts are not always—or perhaps only rarely—distinct the one from the other in the mesial plane. The pyramid—the most caudal of the four areas—usually becomes separated distinctly from the rest, and is linked to the dorsal paraflocculus by the copula pyramidis.

A relatively small space separates the pyramid from the fissura prima in most cerebella, but the narrow bridge which occupies this interval usually undergoes considerable expansion as it is traced laterally. This lateral region is subdivided into three areas A, B, and C, by means of two fissures, which rarely reach so far as the mesial plane.

The anterior area (A) becomes narrower as it approaches the parafloccular fissure. It represents the *lobus lunatus anterior* of the *lobus clivi*.

The area B is distinguished by the fact that its most external part expands in most mammals much more rapidly than the rest; as the result, it usually forms a prominent boss, com-

posed of a feather-shaped group of folia overlapping the paraflocculus. This region seems to be represented in the human brain by the so-called *lobus postero-superior*, which is the lateral part of the *lobus cacuminis*.

The area C undergoes considerable variation in form in different genera. It may be a simple undivided transverse plate of cortex. In many mammals it is a narrow vertical worm-like band, with numerous transverse fissures. In most Apes it is composed of a series of lobules, each composed of numerous long, obliquely-placed folia. It represents the *lobus semilunaris inferior* and the *lobuli graciles* of Human Anatomy. The most difficult problem in the interpretation of the mammalian cerebellum is the explanation of the fate of the cortical band called "copula pyramidis" in the larger members of the various orders.

In the smallest representatives of every order—as for example *Perameles*, *Dasyurus*, *Trichosurus*, and most Marsupials, in all Insectivores and Chiroptera, in most Rodents, in the Dasy podidæ, in *Procavia* of the Ungulata, and in such Lemuroids as *Tarsius* and *Microcebus*—there is a simple undivided band joining the dorsal paraflocculus to the pyramid. In the larger members of most orders the copular band becomes broken up into folia, which are with difficulty distinguishable from the lowermost folia of the area C. It is impossible, without much more complete developmental data than we possess at present, to say whether the copula merely becomes pushed down by the expanding area C, or swells out to form part of the lateral area of the median lobe. The fact that the pyramid in the brain of Man and the Anthropoid Apes is often directly continuous with the so-called *lobus biventralis* and the *amygdala* (tonsil) seems to suggest that these two parts may possibly be formed by the expansion of the folia formed at the expense of the copula pyramidis.

The reader will now have no difficulty in appreciating how unsatisfactory the usual mode of subdividing the cerebellum must be when he recalls that it is based upon the recognition of the morphologically insignificant and unstable furrow which separates the areas A and B as the most fundamental division in the whole organ. For that furrow is the so-called "great horizontal

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fissure." The fissura prima (under the name "præclivalis") is usually regarded as of quite secondary importance.

That the fissura prima (præclivalis) ought to be regarded as the landmark of chief importance in the mesial area of the cerebellum has been suggested independently by Stroud (as the result of developmental studies in *Felis* and *Homo*), by Knithan (after studying the embryology of the cerebellum in *Ovis* and *Homo*), and by the writer (for Comparative Anatomical reasons).

ON THE PRESENCE OF AN ADDITIONAL INCISOR
TOOTH IN A PREHISTORIC EGYPTIAN. By G.
ELLIOT SMITH, *Egyptian Government School of Medicine,*
Cairo.

IN the skull of a man of about 30 years of age, which came from the cemetery in Upper Egypt of the most archaic period, I found a small tooth in the premaxilla, between the first right incisor and the middle line, pushing the intermaxillary suture to the left.

In the absence of any reference library, I am unable to decide whether such an anomaly has been previously noted. I am induced to place it on record by the fact that in none of the anatomical works in my possession which record dental variations is any account of such an extra incisor mentioned; and Tomes, who discusses this question, states that "the lost incisor in man is probably i^2 ".*

In this particular instance I do not think there can be any doubt that the additional incisor is the insignificant tooth on the mesial side of i^1 , so that this case seems to raise the question of the possibility of man's lost incisor being neither the i^3 , as is generally supposed, nor i^2 , as Tomes suggests, but i^1 .

[I described in this *Journal*, vol. xii. p. 142, in a living person, a supplementary incisor which occupied the interval between the upper central incisors. It seemed as if it were mesial in position, but its fang and alveolus could not, of course, be seen.—
W. TURNER.]

* Charles S. Tomes, *A Manual of Dental Anatomy*, 5th edition, 1898, page 531.

NOTE ON A CASE OF MUSCULAR ABNORMALITY
OBSERVED DURING LIFE. By Professor T.
WARDROP GRIFFITH, M.D., *Leeds*.

As shown in the accompanying plate, this seems to be a case of complete absence of the sternal and of a small part of the cla-

vicular portion of the pectoralis major on the right side. There is a chondro-epitrochlearis present, whose tendon can be seen to pass down about three-quarters of an inch in front of the internal

388 CASE OF MUSCULAR ABNORMALITY OBSERVED DURING LIFE.

intermuscular septum, ceasing to be prominent above and in front of the internal condyle where it probably blends with the fascia.

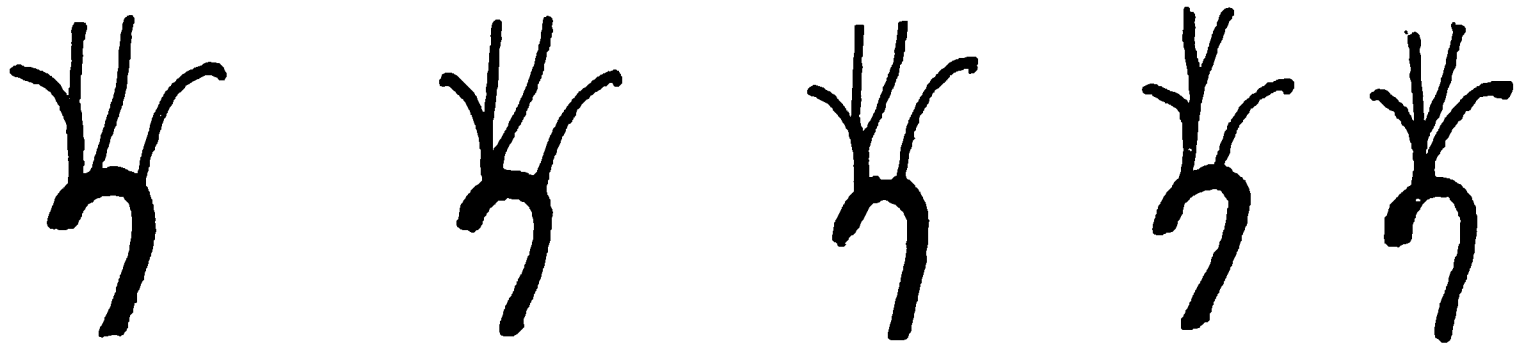
The subject of this anomaly was a twin. The depression was

noticed at or about the time of birth, and it was supposed by his parents that the head of the other child, who was much the stronger of the two, had been resting thereon. The condition causes no inconvenience.

ON THE ARRANGEMENT OF THE BRANCHES OF THE
MAMMALIAN AORTIC ARCH. By F. G. PARSONS,
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I HAVE for a good many years wondered what cause or causes determined the various arrangements of the great trunks arising from the arch of the aorta, and with a view of finding this out, have collected a number of observations on animals dying in the Zoological Society's Gardens, as well as from various museums, and as much of the scattered literature as I have come across. I propose in this paper firstly to tabulate my material, and then to submit the conclusions which I have come to.

The arrangement in the Primates has already been recorded by Keith,¹ who collected the published cases and added to them the results of his own dissections. Most of Keith's records I am using over again, and I have been fortunate enough to dissect some forms of the lower Primates which were poorly represented in his paper; on the other hand, I have adopted a rather different method of tabulation for the sake of harmonising the Primates with the rest of the Mammalia, and for this reason I have not been able to use all his material, since I was not sure under which of my divisions it ought to go.



Man $\frac{1}{2}$.
Gorilla $\frac{1}{2}$.
Anthropopithecus
(Chimpanzee) $\frac{1}{2}$.
Simia (Orang) $\frac{1}{2}$.
Macacus $\frac{1}{2}$.
Other Cercopithecii $\frac{1}{2}$.
Cebus (Capuchin) $\frac{1}{2}$.
Hapale (Marmoset) $\frac{1}{2}$.
Midas (Marmoset) $\frac{1}{2}$.
Mycetes (Howling
monkey) $\frac{1}{2}$.
Chrysothrix
(Squirrel monkey) $\frac{1}{2}$.

Man $\frac{1}{2}$.
Gorilla $\frac{1}{2}$.
Anthropopithecus $\frac{1}{2}$.
Simia $\frac{1}{2}$.
Hylobates
(Gibbon) $\frac{1}{2}$.
Macacus $\frac{1}{2}$.
Other Cercopithecii $\frac{1}{2}$.
Ateles (Spider
monkey) $\frac{1}{2}$.
Mycetes $\frac{1}{2}$.
Lemur $\frac{1}{2}$.

Macacus $\frac{1}{2}$.
Cercocetus
(Mangabey) $\frac{1}{2}$.
Cynocephalus
(Baboon) $\frac{1}{2}$.
Other Cerco-
pithecii $\frac{1}{2}$.
Lemur $\frac{1}{2}$.

Cercocetus $\frac{1}{2}$. Lemur $\frac{1}{2}$.
Ateles $\frac{1}{2}$.
Lemur $\frac{1}{2}$.

¹ *Journ. Anat.*, vol. xxix. p. 453.

In the Cheiroptera all authors seem agreed that the symmetrical bi-innominate arrangement is the constant one, and this agrees with four dissections of my own, two of the fruit bat (*Pteropus*), one of the long-eared bat (*Plecotus*), and one of the pipistrelle (*Vesperugo*).



In the Insectivora the changes are rung on the same bi-innominate arrangement and on one which is very like that of Man save that the left carotid rises farther away from the innominate. The following are the animals on which my generalisation is based.

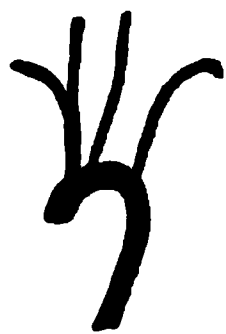


Talpa (Mole) ‡.
Chrysochloris (Golden mole) †.
Erinaceus (Hedgehog) †.

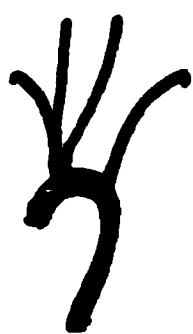


Chrysochloris †.
Erinaceus †.
Centetes (Tenrec) †.
Myogale (Desman) †.
Potamogale †.

The Carnivora are divided into Fissipedia and Pinnipedia; the former, comprising the terrestrial Carnivora, show little variation, and what there is depends on whether the left carotid rises from the cephalic part of the innominate, or whether the two carotids are fused into a common trunk for a short distance after the right subclavian is given off. The Pinnipedia or aquatic Carnivora, on the other hand, although my amount of material is small, seem to have the human arrangement of the great trunks. It will be seen that the family of the Felidæ contains most of the animals in which a short bicarotid trunk is most frequently found.



Phoca (Seal) $\frac{1}{2}$.
Halichærus
(Grey seal) $\frac{1}{2}$.



Meles
(Badger) $\frac{1}{2}$.



Felis leo $\frac{1}{2}$.
F. pardalis
(Ocelot) $\frac{1}{2}$.
Herpestes
(Ichneumon) $\frac{1}{2}$.
Cryptoprocta
(Foussa) $\frac{1}{2}$.
Nandinia
(Palm civet) $\frac{1}{2}$.
Genetta $\frac{1}{2}$.
Arctictis
(Binturong) $\frac{1}{2}$.
Hyæna $\frac{1}{2}$.
Lycaon
(Hunting dog) $\frac{1}{2}$.
Canis familiaris $\frac{1}{2}$.
C. lupus $\frac{1}{2}$.
C. vulpes $\frac{1}{2}$.
Procyon (Raccoon) $\frac{1}{2}$.
Nasua (Coati) $\frac{1}{2}$.
Galictis vittata
(Grisson) $\frac{1}{2}$.
Galictis barbara
(Tayra) $\frac{1}{2}$.
Ictonyx (Zorilla) $\frac{1}{2}$.
Mustela erminia
(Stoat) $\frac{1}{2}$.
Mustela putorius
(Polecat) $\frac{1}{2}$.
Lutra (Otter) $\frac{1}{2}$.

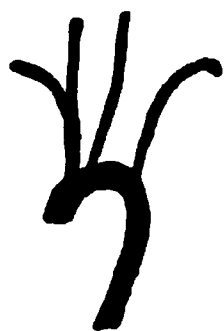


Felis catus $\frac{1}{2}$.
F. tigris $\frac{1}{2}$.
F. pardus
(Leopard) $\frac{1}{2}$.
F. pardalis $\frac{1}{2}$.
F. concolor
(Puma) $\frac{1}{2}$.
F. tigrina
(Margay) $\frac{1}{2}$.
Procyon $\frac{1}{2}$.
Nasua $\frac{1}{2}$.
Gulo
(Glutton) $\frac{1}{2}$.



Genetta $\frac{1}{2}$.

Among the Rodents the left carotid most frequently rises from the root of the innominate. The exceptions will be specially noticed later on.



Gerbillus $\frac{1}{2}$.
Castor
(Beaver) $\frac{1}{2}$.
Lepus ¹ (Rabbit,
occasional).



Sciurus (Squirrel) $\frac{1}{2}$.
Lepus ¹ (normal).
Myopotamus
(Coypu) $\frac{1}{2}$.
Octodon (Degu) $\frac{1}{2}$.
Lagostomus
(Viscacha) $\frac{1}{2}$.
Hystrix
(Porcupine) $\frac{1}{2}$.
Erethizon (Tree
porcupine) $\frac{1}{2}$.
Cavia cobaya
(Guinea-pig) $\frac{1}{2}$.



Sciurus $\frac{1}{2}$.
Erethizon $\frac{1}{2}$.



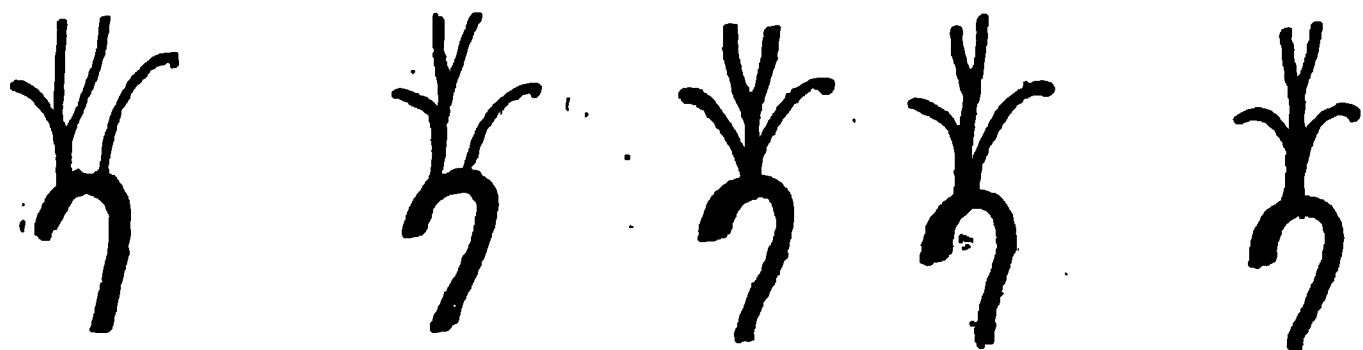
Hystrix $\frac{1}{2}$.



Atherura (Brush-tailed
porcupine) $\frac{1}{2}$.
Dolichotis
(Patagonian cavy) $\frac{1}{2}$.
Dasyprocta (Agouti) $\frac{1}{2}$.

¹ From experience of a large number of class specimens, I have, unfortunately, not kept a record of the proportions.

The Ungulata are remarkable for the way in which all the trunks are compressed; indeed it is most usual to find only one large branch from the aortic arch. Another tendency which will be noticed is for the two carotid trunks to remain fused after both subclavians have been given off. The left subclavian always rises nearer the aorta than the right one does.



Suidæ
(all authors).
Hippopotamus †.
Hyrax †.

Llama ‡.
Giraffa †.
Dorcatherium (Water
chevrotain) †.
Tapirus †.
Hyrax †.

Tapir †. Gazelles ‡.
Antelopes ‡.
Cervus ‡.
Rhinoceros †.

Tapir †.
Cervus †.
Rangifer
(Reindeer) †.
Antelope †.
Ovis (all authors).
Capra
(all authors).
Markhor
(C. falconeri) †.
Bos (all authors).
Equus
(all authors).

With regard to the elephant, Cuvier has recorded a case in which the two carotids arose from the arch together with the two subclavians symmetrically, one on either side of these, as in the accompanying figure.



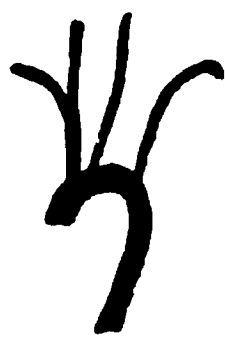
This arrangement has also been noticed by Mayer, but in seven other elephants of which I have records the branches came off as in Man's commonest abnormality, except that the innominate trunk was very short.

Of the arrangement in the Sirenia I have very scanty records, but these are sufficient to show that the tendency is for the

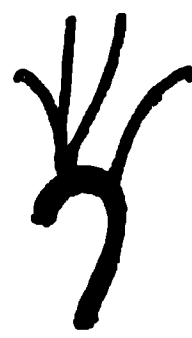
trunks to be as widely, if not more widely separated than they are in Man.



Halicore (Dugong) †.



Manati ‡.



Manati †.

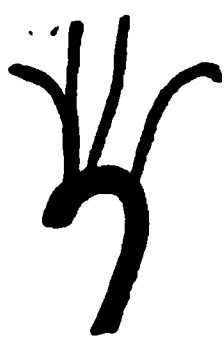
The Cetacea form another order of which records are greatly needed; but, from the small amount of information I have, it seems that a very common, if not the commonest arrangement is to find two symmetrical innomimates, as in the bats.



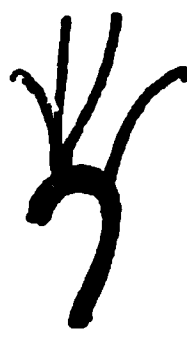
The Edentata have, like the Cheiroptera, Insectivora, Sirenia, and Cetacea, a tendency towards separation of the branches.



Chlamydophorus
(Fairy armadillo) ‡.
Bradypus (Three-toed
sloth) †.
Orycteropus (Aard
vark) †.



Myrmecophaga
(Ant bear) †.
Bradypus †.
Dasypus
(Armadillo) †.
Manis (Pangolin) †.



Myrmecophaga †.

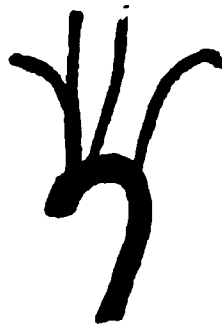
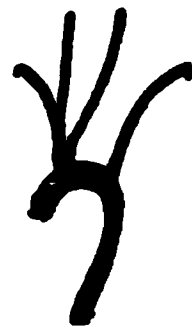


Cholæpus (Two-
toed sloth) †.

The Marsupialia have many varieties of bodily conformation, and, in accordance with this, the arrangement of their aortic branches is very variable; they show, however, some anomalies which, in the present state of our knowledge, are more curious than instructive.

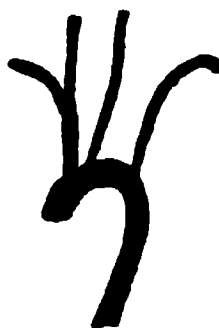


Koala (Marsupial bear) †.

Halmaturus (Bennet's wallaby) †.
Koala †.
Bettongia (Rat kangaroo) †.
Phascolomys (Wombat) †.Halmaturus †.
Dendrolagus (Tree wallaby) †.Macropus (Kangaroo) †.
Petrogale (Rock wallaby) †.
Phalangista (Phalanger) †.Macropus †.
Halmaturus †.
Notoryctes (Marsupial mole) †.
Chæropus (Pig-footed bandicoot) †.

Thylacinus (Tasmanian wolf) †.

Among the Monotremata I have records of two Duck moles (*Ornithorhynchus*) and two Spiny anteaters (*Echidna*); these are the only representatives of the order, and in all four the arrangement of the great trunks is as in Man.



The details tabulated above are very incomplete in many ways, but it is perhaps justifiable to attempt to deduce something from them which may be modified as our knowledge increases. In the first place, it is evident that, with the exception of very homogeneous and comparatively small orders such as the Cheiroptera and Monotremata, nearness of kin does not seem to play any great part in determining the arrangement of the branches of the aorta, and in many cases

individual variation seems much more common than it is in other anatomical details; still, wide as the range of variation often is, there is usually a tendency towards some one plan which may be looked upon as the ideal towards which the different members of the order are striving, and to which they are inclined to 'throw back' whenever the distracting influences allow them. I think that anyone who will take the trouble to go through the foregoing lists carefully will agree with me that the commonest mammalian arrangement is that in which the left carotid rises from the base of the innominate, —an arrangement which it is convenient to refer to as "Man's commonest abnormality" as far as the aorta is concerned.

From this, which may be regarded as the typical mammalian plan, the variations range in two directions, either towards concentration or separation of branches. The first stage towards concentration is that in which the left carotid is united with the innominate for more than half the length of the latter vessel, an arrangement which is usual in the greater number of the Carnivora. The next stage is for the left carotid to come off from the innominate trunk after the right subclavian has been given off, so that there is a bicarotid trunk for a variable distance beyond the innominate proper. This is found in many of the Felidæ and in some of the Ungulata and Marsupialia. A further degree of concentration is where the left subclavian is also fused with the innominate, as is normally the case in the Ungulata, and exceptionally in the Primates, Carnivora, and Rodentia. The first stage towards separation of branches is that in which the left carotid rises from the aortic arch close to, but separate from the innominate; this, which is Man's normal arrangement, is very common throughout the Mammalia, and in point of frequency comes very near Man's commonest abnormality. The next degree of separation is that in which the left carotid rises from the aorta as near the left subclavian as, or nearer than it is to the innominate. This is found in the dugong and the fairy armadillo (*Chlamyphorus*), but is not very often met with. A further degree of separation is that in which all four branches rise separately from the aortic arch; this I think must be extremely rare, as I have only once met with it, and that was in the case of a

marsupial bear (Koala); it is quite possible, too, that this was an individual abnormality, for in another specimen the arrangement was the normal one of Man.

The next arrangement should, I think, be classed under the head of separation of trunks, although it is also one of fusion: it is that in which the left carotid is so far separated from the origin of the right innominate that it fuses with the left subclavian to form a left innominate trunk; this plan is characteristic of the Cheiroptera, some Insectivora, and at least some Cetacea. I have only met with one other modification of the great vessels in mammals apart from those of Man, and that is the symmetrical one in which the two carotids rise by a common stem from the aorta, while the two subclavians rise from the aorta, one on each side of it. This plan has often been looked upon as characteristic of, and confined to the elephant; but, as has been shown above, it was only found in two out of nine specimens, while among the Marsupialia it occurred in the only specimen of the aorta of the Tasmanian wolf (*Thylacinus*) which I have seen.

On comparing the foregoing modifications of the aortic branches in the Mammalia, it is interesting to notice that only one of Man's commoner variations is foreshadowed, and that is the commonest one, in which the left carotid rises from the root of the left innominate, and to this I propose to return later on. I have never seen in the lower mammals an example of a vertebral rising from the arch, nor of that interesting abnormality of Man in which the right subclavian rises last of all the branches. I should therefore regard these human abnormalities at present as quite new and tentative attempts to meet some changed conditions in Man,—as progressive variations, in fact, which may or may not become more common as time goes on. When one considers the great physical changes which the erect position must have caused the circulation, one can only wonder at the similarity of the blood-vessels of Man to those of other mammals.

With regard to the immediate causes which produce the different arrangements of the aortic branches of mammals, it has been suggested that their separation is associated with increased breadth of the thorax, while those animals which have

thoraces compressed from side to side are more likely to have their aortic branches fused. It is only necessary to take two or three well marked cases to see that this is undoubtedly a very important cause, but I would suggest that only that part of the thorax in which the arch of the aorta lies—the anterior or cephalic part—concerns us, for in some of the Rodents, such as the Agouti, for example, the anterior part of the thorax is very narrow, while the posterior part broadens out immensely. Indeed, I have every reason to believe that it is the comparative breadth or narrowness of the anterior outlet of the thorax which is the chief determining factor. In the more specialised Ungulates, such as the Bovidæ, Equidæ, and Cervidæ, the outlet of the thorax is often twice as deep as it is broad, and these animals show the maximum fusion of the great vessels. In the Hyrax, which is regarded as an archaic and more generalised Ungulate, on the other hand, the outlet of the thorax is 1 inch deep and $\frac{3}{4}$ inch broad,¹ and here we find that the left subclavian rises separately from the aorta, and not from a common stem with the other branches.

If we next take an animal such as the fruit-bat, we find that the outlet of the thorax is nearly three times as broad as it is deep, and in this animal the left carotid is so far removed from the innominate that it blends with the left subclavian to form a left innominate trunk.

Again, in aquatic animals the thorax and its outlet are usually flattened dorso-ventrally, and broadened from side to side, and these (*e.g.*, Cetacea and Sirenia) show a tendency to separation of trunks ; moreover, in orders which have one or two water-loving forms, we often find that these forms are the ones which have the greatest separation of trunks of any in the order. Examples of this are the Seals among the Carnivora, the Beaver among the Rodentia, and the Hippopotamus among the Ungulata, though I am bound to state that the Otter does not bear out this generalisation. It would be quite easy, had I the space, to multiply examples showing the coincidence

¹ I am quite aware of the fallacy of contrasting the breadth of the thorax with its depth, but I can think of no other more satisfactory basis of comparison in animals differing so widely in bodily shape as the mammals do. A standard such as the length or weight of body would, I fear, be more open to objections.

between a broad thorax and its outlet on the one hand, and separation of aortic branches on the other; these examples are so numerous that it seems justifiable to regard the arrangements as cause and effect; indeed, the same breadth of body seems to exert an influence upon the pelvic arteries as well, for, roughly speaking, the orders which show separation of the branches of the aortic arch are those in which common iliacs are found, while, when the aortic branches are fused, the external and internal iliacs usually rise separately from the termination of the aorta.

There are, however, certain cases in which the breadth of the thorax seems to fail to account for the great difference in the arrangement of the arteries; the Agouti and the Guinea-pig, for instance, are Rodents not very distantly related, and in both the shape of the thorax is alike; it is narrow anteriorly, broad posteriorly, and yet the Guinea-pig has its aortic branches arranged as in Man's commonest variation, while in the Agouti the left subclavian rises from the root of the innominate (see p. 391).

In the Guinea-pig, however, the aortic arch lies opposite the second and third thoracic vertebræ, while in the Agouti it is opposite the fourth and fifth.

I am at present carefully examining the relation of the aortic arch to the vertebræ in all the mammals which come in my way, and I have seen enough to make me strongly suspect that the nearer the arch is to the thoracic outlet the more likely are the branches to be separated; and if these observations are borne out by other observers, we must hold that there are at least two causes acting to modify the details of the branches of the aortic arch,—firstly, the breadth of the anterior part of the thorax and its outlet; and secondly, the position of the arch itself.

Having discussed the causation of the various arrangements of the branches of the aortic arch, it will be well to consider the question as to whether the commonest abnormality of Man's aortic arch should be regarded as a reversionary variation to a plan which is the normal in so many of the other mammals, or whether it should be looked upon as a similar and parallel effect produced by similar causes. Keith regards it as of "no more morphological worth than the degree of interdigital webbing."

Personally, I should be unwilling to express any opinion without further facts, and all I wish to do here is to suggest to those who happen to read this paper that it will be worth while to carefully examine those cases in Man in which the left carotid rises from the root of the innominate, with a view to finding out (1) whether the transverse diameter of the outlet and upper part of the thorax is diminished, and (2) whether the aortic arch is lower (more caudal) in position than it usually is. If the results are negative, I think the abnormality may be regarded as an instance of reversionary variation, though, as I have already said, there are no grounds for believing that the other common human abnormalities have any such meaning.

With a view to assisting in such investigation, I may state that I have found that the breadth of the outlet of Man's thorax is usually just twice as great as its depth, or antero-posterior measurement; while, as is well known, the arch of the aorta is opposite the fourth thoracic vertebra.

THE RELATIVE WEIGHTS OF THE RIGHT AND LEFT
SIDES OF THE BODY IN THE FŒTUS. By T. G.
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THE object of the following paper on the subject of the relative weights of the thoracic and abdominal viscera on either side of the mesial plane of the body in the foetus is to establish the fact that in the foetus after the fifth month there is a marked preponderance in weight of the right side over the left, which is to be ascribed to the disposition of the abdominal viscera. Owing to the difficulty in obtaining a sufficient number of specimens, the investigation could not be carried out upon foetuses of an earlier age. From among the numerous weighings which I have made, it will be only necessary to quote the averages, since a detailed account would prove tedious; and moreover, the differences in weight obtained in each case did not vary in any proportionate manner with the age of the specimen.

Numerous investigators have endeavoured to decide whether there is any difference in weight of the corresponding limbs on the right and left side in the new-born child and in the foetus, but as yet no definite agreement exists amongst them, although weighings have been made both of the limbs as a whole, and of the bones and muscles separately. Harting (1) states that at birth no difference in length between the upper limbs is present, but that the bones of the right side are the heavier as a result of hereditary transmissions. Bischoff (2), Gaupp (3), and Theile (4) agree with the latter part of this statement, and indeed in one case Theile found that the right arm of a new-born child weighed as a whole 4 per cent. more than that of the opposite side. Gaupp, however, qualifies his opinion by stating that the difference does not exceed the limits of possible error; and when his cases and those of Bischoff are examined, it is found that out of a total of eleven cases the right arm was the heavier in three, the left in three, and that complete equality existed in six cases. Theile, weighing the muscles separately, found that no difference existed between those of the right and left arm taken as a whole,

but that differences existed in the weight of certain groups. Biervliet (5), on the other hand, found that a difference of as much as 1.85 grammes existed between the total weights of the muscles of the right and left upper limb, the right being the heavier of the two. In the lower limbs a similar difference in results obtained is found; thus, to quote only one authority, Bischoff out of three cases found the right lower limb the heavier in one, and the left in two.

From this mass of conflicting evidence I am forced to the conclusion that no real differences exist, and that when any has been found, it has been due to unavoidable errors in the preparation of the specimens, and my own observations confirm me in this opinion. After weighing as a whole the limbs of eight fœtuses, I was unable to detect any constant difference; and even had I found such to exist, I would not be inclined to lay stress upon the fact, since the smallest difference in moisture would readily account for it. A similar remark applies to weighing of the muscles separately, though in one fresh fœtus in which I weighed the muscles of each upper limb as a whole, and also the biceps muscles separately, no difference was found. More importance, then, should be laid upon a difference in weight of the bones of two sides, but out of three cases in which weighings were made of these in both the upper and lower limb, I could not detect the smallest difference. In a fourth case I even weighed the diaphyses of the humerus, radius, and ulna of one side with those of the other, and also the diaphyses of the femur, tibia and fibula of the two sides, and found an absolute equality in the weights obtained.

As early as 1863 a paper was published upon the subject of the weights of the thoracic and abdominal viscera by the late Professor Struthers (6), and appeared in the *Edinburgh Medical Journal* for that year. He confined his attention to the examination of adults and of children of from two to three years of age, and though he does not express himself definitely upon the point, appears to have been of the opinion that the large size of the left lobe of the liver in the fœtus caused the viscera on that side to be of an equal weight with those on the left. His object was to prove that the centre of gravity of the body lies to the right side of the mesial plane even when the limbs have

been removed, and the weighings which he has given in proof of the point are, I believe, in the main reliable. However, the methods of hardening the viscera were then very imperfect; and moreover, many of the organs were only divided and weighed after they had been removed from the body and had lost their shape. But if the same fact can be shown to hold good for the foetus in which the viscera have been hardened by formalin and accurate mesial sections made, it will, I believe, be *a fortiori* true in the case of children and adults; and the point, in addition to being of some slight importance from an obstetrical point of view, as possibly being a determining factor in the different varieties of vertex presentations, will also be of interest in the general study of animal equipoise.

As would be expected, the weight of the thoracic viscera on either side of the mesial plane varies with the age of the foetus. During the fifth and sixth months the weight on the two sides does not differ much, but after this the left side steadily gains upon the right, till at full term it averages about 56 per cent. of the entire weight of the thoracic viscera, and is heavier than the right side by about 92 grains. The difference is due in part to the larger size of that portion of the thymus gland which lies to the left of the mesial plane, but principally to the position of the heart, for the right lung is heavier than the left in even a greater proportion than in the adult. Thus, in one foetus of about six months, the right lung weighed 60 grains and the left 47 grains, while the left portion of the heart weighed 23 grains as against 15 grains for the right portion,—the total difference on the two sides being only 5 grains, and that in favour of the right side. In another foetus of eight months, the right lung weighed 118 grains and the left 103 grains; the right portion of the heart weighed 30 grains and the left portion 135 grains,—the total difference on the two sides being 90 grains in favour of the left side.

It is possible that during life the left side would preponderate still more over the right on account of the chambers of the heart containing more blood, but any such difference must be very slight, since it is a peculiarity of the foetal heart that after death the left chambers contain nearly as much blood as the right.

In the abdomen in the foetus the space allotted to viscera on

either side of the mesial plane is the same, for if casts be made of the entire visceral mass enucleated *in toto* from the abdominal cavity, it is found that after making a mesial section the weight of the two halves is identical, or that in any case there is not a difference of more than 1 per cent. Any difference in weight on the two sides is therefore due to the different grouping of the hollow and the solid viscera, the former being, for their bulk, light as compared with the latter. After an examination of several fœtuses of from five to eight months, it was found that the right side of the abdominal visceral mass represented from 56 per cent. to 53 per cent. of the entire weight of these viscera, and was heavier than the left by from 105 to 300 grains, the excess of weight being due to the right portion of the liver. It is sometimes stated that during fœtal life the right and left lobes of the liver are of almost equal size; and indeed, on opening the abdomen, they often appear to be so at first sight; but the antero-posterior depth of the right side, especially towards its lower free margin, is always much greater than that of the left side, and consequently the right portion is much the heavier. Thus, in one case the right side was found to be nearly three times as heavy as the left, and at full term it was more than once found to be a little over twice the weight of the left side.

The kidneys and suprarenal capsules of the two sides are almost exactly equal in weight, but the portion of the intestinal tract together with the spleen on the left side weighs more than the intestinal tract on the right side. The difference is, however, usually slight as compared with the difference in weight of the two sides of the liver. Towards full term, indeed, the accumulation of large masses of meconium may cause the total weight of the viscera on the left side to become almost equal with that on the right side; but since this is only a temporary condition it cannot be held to invalidate the general result, which may be stated as follows:—From at least the fifth month of fœtal life onwards the centre of gravity of the body is placed to the right side of the mesial plane, the thoracic and abdominal viscera on this side representing 52·6 per cent. of the total weight of the viscera, as compared with 47·4 per cent. on the left side. The child therefore enters upon its extra-uterine existence with a marked right-sided bias.

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THE COMPARATIVE HISTOLOGY OF THE URETHRA.

By J. STRICKLAND-GOODALL, M.B. Lond., *Senior Demonstrator of Physiology and Biology, Middlesex Hospital, London.*

(From the Biological Laboratories of the Middlesex Hosp. and City of London Coll.)

THE histology of the urethra, both human and comparative, is, judging from the accounts given of it in existing text-books,¹ a subject to which but little attention has been paid; and inasmuch as, in the first place, the accounts given of its structure differ very considerably in the different standards of physiological truth, and in the second place, it does not seem very clear whether the accounts given refer to the human urethra alone or to urethras in general, it appears to be a subject worthy of further consideration. The following work was carried out at the suggestion of Dr R. A. Young.

Up to the present I have thoroughly investigated the structure of the urethra in the Rodents, and have examined animals representative of all sub-classes. I have also examined representatives of the Ungulata, Carnivora, Insectivora, and

¹ How much these accounts differ may be seen from the following. STÖHR, *Text-Book of Histology* (pp. 295 and 296), states that the urethra consists of a muscular and mucous coat, and that the latter varies in structure in different positions, the chief differences being in the epithelium, which is described as follows:—(a) Prostatic like bladder, (b) Membranous stratified columnar, (c) Cavernous simple columnar, (d) In front of fossa navicularis, stratified.

KLEIN and NOBLE SMITH, in their *Atlas* (page 279), state that (a) The lower half of the prostatic and membranous portions are lined by stratified pavement epithelium, (b) The upper half (of prostatic portion ?) by stratified transitional, (c) In front of bulb by columnar epithelium. These authors also state that the epithelium differs in different urethras and at different times. (d) In fossa navicularis and in front, stratified pavement.

BRASS and YOUNG (page 146, figs. 9 and 10, page 156, figs. 1, 2, 6, 7, 8), quoting apparently from Ziemke, describe and figure the epithelium as composed of two or three layers of cells, the superficial being elongated and cylindrical.

While BOHM and DAVIDOFF (page 333) give the following: (a) Prostatic portion like bladder, (b) Membranous part either (i) like prostatic or (ii) pseudo-stratified, (c) Cavernous pseudo-stratified, (d) Fossa navicularis and in front, stratified.

Anthropoidea. The following is a list of the animals examined up to the present.

MAMMALIA.

Rodentia—

- (a) Myomorpha—(1) *Mus musculus*, (2) *Mus decumanus*.
- (b) Mystricomorpha—(1) *Cavia apaerea*.
- (c) Lagomorpha—(1) *Lepus timidus*, (2) *Lepus cuniculus*.
- (d) Sciuromorpha—(1) *Sciurus vulgaris* (i).

Carnivora—

Felis domesticus.

Insectivora—

Erinaceus europeus (ii).

Anthropoidea (iii).

Ungulata—

Ovis aries.

(i) (ii) (iii) not dealt with in this article.

As regards methods employed, the specimens were hardened in Müller's fluid three weeks, alcohol (85 per cent.) three days, and were either embedded in paraffin and cut on a rocking microtome, or cut in gum; practically every section was examined and mounted.

Many different varieties of stain were employed, the combinations most frequently employed being Van Giesen, Hæmalum and Eosin, and Picro Carmine,—for micro-photographic purposes the first mentioned being very much the best.

I now proceed to consider each of the above types in detail.

Mystricomorpha.—

In *Cavia apaerea* (Guinea-pig) the urethra opens on the antero-ventral aspect. Anteriorly, it consists of a mucous membrane composed of thick stratified epithelium of four to eight rows of cells, the superficial cells being for the most part flattened, the deep cells columnar. The epithelial lining becomes continuous with the surface epithelium anteriorly and ventrally, so that on section the urethral outline is T-shaped. External to the epithelium is a basement membrane and a well marked layer of circular muscle; there is no sub-epithelial connective tissue, and no longitudinal muscle distinct from the general muscle of the cavernous tissue. Dorsally, the




urethra is protected by a large oval piece of hyaline cartilage. As the urethra is traced backwards it is found to become very widely dilated, while its mucous membrane presents two very large folds, which project inwards from its dorsal aspect, and numerous smaller folds, situated chiefly on the ventral floor. Structurally, the urethra presents precisely the same features as those described above, but the circular muscle presents in places large venous spaces. Dorsally, a large crescentic space



FIG. 1.—Transverse section through penis of Guinea-pig (*Cavia aparea*).—(a) longitudinal muscle; (b) C-shaped structure of muscle (mainly longitudinal) and yellow elastic tissue surrounding urethra; (c) large blood-space; (d) blood-spaces in supporting tissue of urethra; (e) urethra; (f) layer of stratified epithelium lining urethra—note longitudinal glands cut across; (g) circular muscle of urethra; (h) longitudinal muscles.

is seen, lined by stratified epithelium, and formed by the prolongation inwards of the surface epithelium.

In the ensuing parts, the urethra retains the same essential features, but the mucous membrane is thrown into numerous low longitudinal folds, into the intervals between which very many glands are seen opening. The bulk of these glands appear to run longitudinally, and hence are seen in transverse section, each appearing circular in outline, and being composed

of a single layer of clear columnar cells, resting on a cellular basement membrane, the nuclei of which stain well. The circular muscle coat in this situation is particularly well developed. On following the urethra backwards, it is found to become more or less egg-shaped, and to be suspended in a circular space, bounded above and laterally by a thick -shaped piece of muscle, below by a thin layer of circular muscle which bridges over the ends of the . Dorsally, the urethra is attached by loose cavernous tissue to the -shaped structure mentioned above, while ventrally it is attached to the thin band of circular muscle by some of its own circular fibres, diverging to become continuous with the circular fibres above described. The mucous membrane is thrown into numerous small folds, and is lined by a fairly thick stratified epithelium; a fair number of glands can also be seen. There is a moderately well marked circular muscle-coat, in the midst of which numerous small arteries can be seen (fig. i). As the urethra passes backwards, its outline is found on section to be definitely T-shaped; its mucous membrane, as before, presents many folds, but no glands are seen opening into the urethra between them. The epithelium is still of the stratified pavement type. The circular muscle-coat is now very badly developed, and the whole urethra receives but little support. Farther backwards, the urethra widens out transversely, and its folds of mucous membrane become much less prominent. The epithelium is composed of several layers, but is thinner than in the preceding parts. Basement membrane and circular muscle all occur as before, but in the latter numerous branching glands are found. The whole urethra has much thinner walls than in any other position. As the urethra nears the bladder it again narrows down and its lumen appears as a transverse slit, its lining epithelium is thick and many of its superficial cells are columnar. Its circular muscle-coat is unusually thick and well developed, and presents a few longitudinal fibres mingled with it.

The Myomorpha.—

In the Rat (*Mus decumanus*) and the Mouse (*Mus musculus*) the urethra is particularly complicated and difficult to in-

investigate on account of the peculiar bend in the penis and the complexity of adjacent structures. Anteriorly, the urethra appears in section as an oval transverse opening; its mucous membrane is lined by a thick stratified epithelium of four to six layers of cells, the superficial layers of which are flattened and horny, the deeper columnar. The latter have well marked oval nuclei, and stain well. The basement membrane is thick and well marked, and underneath it is a very thin layer of sub-epithelial connective tissue, which in places is altogether absent. External to the connective tissue is a well marked layer of circular muscle; no longitudinal fibres can be made out. The circular fibres are least developed dorsally where they are encroached upon by a dorsal rod of hyaline cartilage, round which a few of the fibres in places appear to pass. Ventral to the urethra is an oval space, lined by stratified epithelium, which becomes continuous with the surface epithelium ventrally. A little posterior to the above, the urethra is found on section to be something like the head of an anchor ∇ . Its mucous membrane is thick and conspicuous, the epithelium being composed of from six to eight layers of cells, the superficial of which are flattened as in the previous section; the basement membrane and sub-epithelial connective tissue have much the same features. External to this is a well marked layer of circular muscle, the most internal fibres of which closely follow the outline of the epithelium, while a few of the more external (or peripheral) fibres having closely followed the urethral epithelium on the ventral and lateral aspects, diverge from it dorsally to invest the os penis. As the urethra is traced backwards, it is found to become more closely applied to the os penis, which is now expanded considerably. The mucous membrane presents numerous longitudinal folds, which project conspicuously into the lumen; the epithelium is thick and stratified; the sub-epithelial connective tissue is reduced so as to be practically absent, while the circular muscle-fibres can be divided into three groups—(i) the most internal, which follow the outline of the epithelium; (ii) the middle layer, which forms a strong thick circular coat, which is well marked ventrally and laterally, but thin and poorly developed dorsally; (iii) the external layers consist of a few

fibres, which are closely applied to the urethra ventrally, but diverge dorsally to embrace the os; as one passes backwards some longitudinal fibres are found mingled with these on the ventral aspect (fig. ii).

Still further back, the urethra becomes elongated vertically and the longitudinal folds of mucous membrane become still more prominent; the epithelial lining is stratified, but its superficial cells are in places columnar. The circular muscle is still present, but is thinner than in the preceding section, and its fibres cannot be differentiated into three layers; no longitudinal fibres at all can be made out. Posteriorly, the urethral

FIG. ii.—Transverse section through glans penis of *Mus musculus*.—(a) prepuce; (b) erectile hair; (c) os penis; (d) urethra; (e) frenum; (f) layer of muscle following outline of epithelium; (g) layer of circular muscle; (h) layer of muscle diverging to surround os penis dorsally.

opening becomes irregular in outline, its mucous membrane being thrown into many irregular folds; its epithelium is thick and stratified, the basement membrane is prominent, while the circular muscle in part follows closely the outline of the epithelium, while ventrally it becomes divided into two layers by a quantity of loose cavernous tissue, composed of muscle, elastic and fibrous tissue, containing many small arteries with thick muscular walls; of these two layers, the inner closely follows the epithelium, the outer forms a thick circular coat; dorsally these two coats are contiguous.

Lagomorpha.—

In the Rabbit (*Lepus cuniculus*) and the Hare (*Lepus timidus*) the urethra is characterised by being wide and dilated, and having little if any support throughout its entire length. The epithelium throughout is particularly thin and delicate. Anteriorly, the urethra appears in transverse section as an irregularly oval opening, its lining membrane being thrown into a few irregular longitudinal folds (fig. iii). The epithelium is extremely thin, and consists of four or five layers of small cells, the superficial being slightly flattened and cornified, the deeper ones columnar and staining readily; the basement membrane is very

FIG. iii.—Section through penis of *Lepus*.—(a) stratified epithelium covering surface; (b) cavernous tissue; (c) dilated urethra—note thinness of epithelium and absence of any definite supporting tissue.

thin, and can hardly be said to exist; external to it is a fairly definite layer of circular muscle, better marked in the Hare than the Rabbit, no sub-epithelial connective tissue or muscularis mucosæ can be made out. Slightly posterior to the above, the urethra appears as an obliquely transverse slit, whose mucous membrane presents longitudinal folds, which are much more numerous than in the preceding section. The epithelium is extremely thin, and consists of a single layer of long columnar cells resting on an ill-defined basement membrane; these cells

taper at their bases, and numerous small polyhedral cells fill in the intervals between them. The columnar cells have a very conspicuous striated free border and in places appear almost ciliated. External to the basement membrane is an ill-defined layer of circular muscle, best developed on the ventral aspect, and in some cases being quite absent dorsally. In places, a few longitudinal fibres are found mingled with the circular muscle.

On tracing the urethra backwards, it appears in section as a more or less crescentic slit; the epithelium retains the same essential features as before, some of the cells being very long and columnar. The circular muscle is now mixed with a good many longitudinal fibres, the epithelium being much better supported than anteriorly. Posteriorly, the urethra becomes somewhat L-shaped, but its mucous membrane and muscle coat remain essentially the same.

Carnivora.—

In the Cat (*Felis domesticus*) the urethra is wide and dilated anteriorly, and somewhat T-shaped in section. Its mucous membrane is thick and well supported, the epithelium consisting of several layers of superimposed cells, the superficial ones being for the most part flattened or polyhedral and resting on three or four layers of irregular polyhedral cells, which in their turn are superimposed upon a layer of cells of more columnar shape. These rest on the basement membrane. Occasionally in places a columnar or pyriform cell may be seen extending up to the surface. Under the basement membrane is a thick layer of circular muscle, which forms a strong support to the urethral epithelium, its fibres closely following its outline. This muscle is characterised by the size of its nuclei. External to the muscle is a quantity of cavernous tissue containing many large venous SPACES, while immediately dorsal to the urethra is seen a bony structure invested by a layer of muscle. Passing backwards the urethra becomes star-shaped, and is found to be much less supported by the circular muscle, the cavernous tissue becomes looser and its venous spaces larger and more conspicuous, an area of it surrounding the urethra, and now being encircled and cut off by a layer of circular muscle extending

up dorsalwards to embrace the os penis, which is now much expanded. The epithelium has the same essential features as before, but consists of fewer layers of cells, and contains a larger proportion of columnar ones. On tracing the urethra backwards, it is found to have the same essential structure as before, but the epithelium, though still definitely compound, consists of only three or four layers of cells, and its superficial cells are now frequently found to be columnar. Still farther back the urethra becomes †-shaped; its epithelium becomes thick and stratified; its circular muscle is very strongly developed indeed, while external to this is cavernous tissue, with many longitudinal muscle-fibres and small arteries, the whole being encircled by a layer of circular fibres. Towards the bladder the cavernous tissue about the urethra increases in amount, first making its appearance on the ventral aspect, and being quite absent dorsally. Proceeding backwards, the urethra becomes oval and widely dilated, and appears to be suspended in the centre of a large oval mass of cavernous tissue of the loosest description. The epithelium is thick and stratified, and the circular muscle well marked. Just before reaching the bladder, the urethra becomes horseshoe-shaped, and finally irregular in outline, owing to the entry into it of many branched glands. The epithelium has the same essential features as before, but the inner layer of circular muscle is much intersected by the glands.

Ungulata.—

In the Sheep (*Ovis*), the urethra is prolonged forwards in front of the glans penis as a longer slender filament known as the VERMIFORM process; this, on transverse section, is seen to consist of (i) a layer of stratified epithelium, the deeper cells of which are deeply pigmented; (ii) a thick layer of circular muscle; and (iii) a mucous membrane, thrown into many longitudinal folds. This mucous membrane is lined by a thick stratified epithelium, the superficial layers of which are flattened and somewhat horny, resting on a basement membrane, under which is a small amount of areolar connective tissue and a definite muscularis mucosæ. Towards the posterior part of the vermiform process the urethra is found to be considerably elongated in a vertical diameter, while laterally are seen two large oval masses of

muscle, yellow elastic and white fibrous tissue (fig. iv). The urethral mucous membrane presents the same features as before, only there is little sub-epithelial areolar tissue; tracing the urethra backwards, it is found to become asymmetrical in position, and to be enclosed in a triangular area, which is bounded by a solid epithelial layer, composed of many cells (fig. v), the deeper and more superficial layers of which are deeply pigmented. This epithelium sends out solid outgrowths, which extend into the adjacent structure (fig. v). In the posterior part of the

FIG. iv.—Section through posterior part of vermiform process of penis of Sheep.—
(a) stratified epithelium; (b) lateral mass of muscle, elastic and fibrous tissue; (c) urethra; (d) stratified epithelium of urethra; (e) circular muscle of urethra.

glans the urethra is somewhat dilated, and the folds in its mucous membrane are much less prominent; its histological features are, however, identical. The solid epithelial layer above described is, however, found to lie quite remote from the urethra, and is not far internal to the surface. Tracing the urethra back to the bladder, it is found to be circular in outline, and to be surrounded on all sides by large venous spaces. The mucous membrane is thick and well marked, and thrown into numerous folds; the epithelium is thick and stratified, consisting of six to twelve rows of cells; there is a definite basement membrane and a good deal of circular muscle, but few if any longitudinal

fibres can be seen. Very few glands indeed can be seen opening into the urethra. The thickness of the epithelium appeared to differ considerably in different specimens examined. In writing the above account, I have purposely refrained from giving any actual measurements of the thickness of the epithelium, size of the superficial and deep cells, etc., as such measurements, when made from a *hardened* specimen, are probably utterly

b

FIG. v.—Section through penis of Sheep, in region of glans.—(a) urethra; (b) solid epithelial structure surrounding urethra; (c) solid epithelial growth permeating glans substance; (d) muscle fibres following outline of epithelial growth.

fallacious, and hence valueless,—the apparent thickness being largely dependent upon the nature of the hardening fluid used.

SUMMARY AND CONCLUSIONS.

1. The histological structure of the urethra differs considerably in different animals.
2. In all the animals examined (except the Lagomorpha) the

epithelium is compound throughout, and in no case is a simple columnar epithelium found, but the characters of the superficial cells vary considerably in different animals, and in the same species of animal at different times.

3. The sub-epithelial connective tissue in no case forms a distinct layer, and in most cases is practically non-existent.

4. There is no longitudinal muscle-coat, internal, to the circular muscle, and no distinct muscularis mucosæ can be differentiated off from the circular muscle.

5. The dilatability of the urethra differs very widely in different animals.

In conclusion, I have to thank my friend Mr Frank Goddard for the time and trouble he has taken in photographing many of the specimens, and in making the excellent lantern slides used in illustrating the demonstration given before the Anatomical Society of Great Britain and Ireland; also Dr R. A. Young, for his initial suggestion, and for his subsequent kindness; and Mr H. Acton, for the trouble he has taken in mounting and photographing some of the specimens. To one and all of these I tender my sincere thanks.

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A SUPRA-CLAVICULARIS PROPRIUS (GRUBER). By
P. P. LAIDLAW, *St John's College, Cambridge.*

ON the left side of the neck of a female subject in the Cambridge dissecting-room I found an excellent example of this rare muscle. It rose by a flat tendinous expansion from the surface of the cervical fascia overlying the sternal origin of the sterno-mastoid muscle and the sterno-clavicular joint. The fibres soon became fleshy, lying at first on the upper surface of the clavicle, but as they passed laterally they spread slightly on the superficial aspect of the clavicular fibres of the trapezius, into the fascial sheath of which they were inserted at about the level of the acromion process.

The belly of the muscle is closely applied to the clavicle, whose curvatures it follows. The descending supra-clavicular branch of the fourth cervical nerve passes beneath it; between its deep surface and the clavicle a small twig from this nerve, which leaves the trunk a little above the level of the muscle, enters on its deep surface and is distributed to it.

There was no trace of a corresponding muscle on the other side.

The muscle corresponds with the description given by Gruber (in *Reichert's Archiv*, 1865, p. 703) of his *supra-clavicularis proprius, sive tensor fasciæ colli*. Like his specimen, and that described by Dubar (*Bulletin de la Société Anatomique de Paris*, v. 388), it was so arranged that, when it acted, its curvature would disappear, and it would make tense the fascia of the neck.

As far as the literature is available to us, this seems to be the ninth case on record, the others being published by Knott, Bardeleben, and Le Double.

However, there appears to be no specific difference between this muscle and that which Hyrtl described (*Sitzungsberichte der K. K. Akademie in Wien*, 1858, xxix. p. 265) under the name sterno-clavicularis, the only ground of distinction being that the latter extends medially to the front of the sternum; a very slight dissection of the tendon of origin could easily have given it the appearance of a sternal extension. This latter

is much the commoner form, however, as since its first description by Haller (*Elem. Physiol.*, 1766, iii. 46) it has been noted by at least fifteen observers, and two of these give statistics from which its frequency seems to be about one in thirty bodies. This is an unusually high degree of frequency, and one which the records in the Anomaly Book kept in this School do not bear out.

As to its nature, whether a displaced fascicle of platysma or a displaced intermediate portion of the sheet of muscle of which cleido-mastoid and trapezius are dismemberments, this specimen does not furnish conclusive evidence to decide. Its nerve supply, however, correlates it with the trunk ventral musculature rather than with that of the seventh pair, of which the platysma is an extension.

It is interesting to note that this slip coexisted with a fascial insertion of a slip of levator anguli scapulæ over the serratus posticus superior, and with a curious condition of the thyroid body. Its two lateral lobes, which were very much enlarged, were quite separate from each other. In the interval between them the median lobe, which was small, hung down, lying on the front of the cricoid cartilage and the uppermost ring of the trachea, quite unconnected with the lateral lobes, but pendent at the extremity of a continuous cord which ascended over the median notch of the thyroid cartilage and pierced the thyro-hyoid membrane in the middle line behind and below the hyoid bone. No visible trace of the canal survived in this persistent remains of the thyro-glossal duct.

EMARGINATION OF THE PATELLA. By the Rev.
F. C. KEMPSON, M.B., *Caius College, Cambridge.*

A COMMON variation of the patella, which has, however, not to my knowledge been publicly noticed, is the presence of a depression in the upper portion of the outer margin of the bone. In typical specimens, the margin of the bone is concave from a point about half an inch to the outer side of the middle line to a point half way down the outer margin of the bone, that is to say, at its widest point. A slight tubercle marks the upper limit of the depression, and at its lower limit there is a sharp

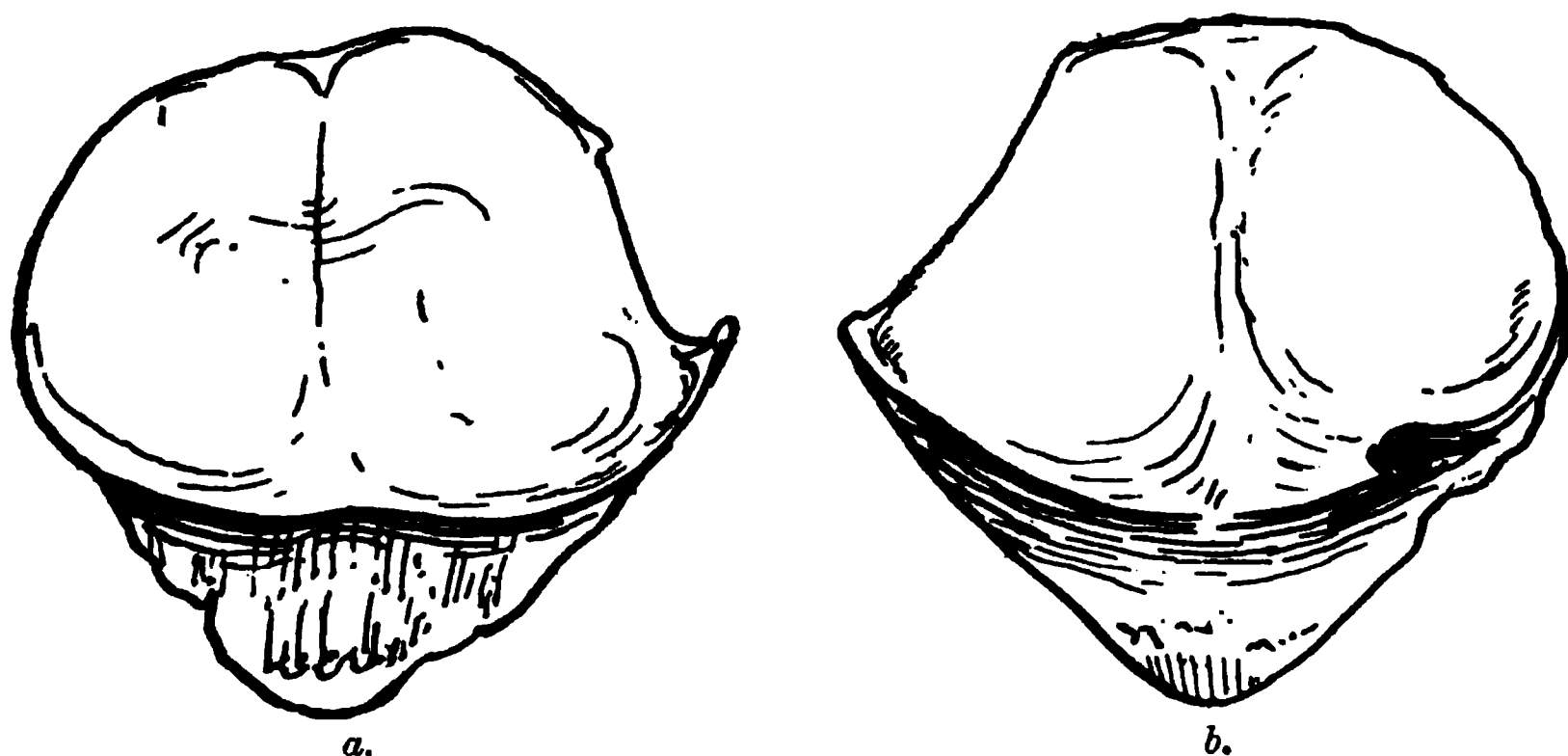


FIG 1.—Two patellæ having well marked indentations and spinous processes.—
(a) A right patella, modern, from a student's set of osteology; (b) a left patella of an ancient Egyptian.

spinous process directed upwards and outwards. The margin of the concave portion is usually smooth.

Every gradation is found between patellæ having well marked notches as above described, and those which show no trace; but however faint the indentation may be, it always shows signs of a sharp angle, if not a spine at its lower extremity. These indentations occur in small and ill-marked as well as in large and well-defined patellæ, and in both ancient Egyptian and in modern specimens. One very small patella, which is specially deficient on its inner sides, has a clear depression, and an especially prominent, though not very sharp, spine. In another large patella the whole notch is placed on what looks like a distinct outgrowth upwards and outwards from the main mass

of the bone, and the indented part of the margin is very much roughened. In this case it seems as if there had been some degree of osteo-arthritis.

Why this depression should occur on some patellæ and not on others I will not venture to suggest, but it is certainly connected

FIG. 2.—Dissection to show the insertion of vastus externus. The upper part of the muscle A is divided from the lower part B by an incision running parallel to the fibres of the muscle. The cut surface of the lower part is shown with the muscular fibres inserted into the two surfaces of the tendon C, which is inserted in the upper and outer part of the margin of the patella.

with the insertion of the tendon of vastus externus, the lower limit of which is marked by the spinous process. The upper fibres of this muscle will on examination be found to form a thin aponeurotic tendon inserted into the upper margin of the bone behind the rectus, while the lower fibres are inserted into a much shorter flat tendon, which at its beginning is embedded in the muscle substance, but which is clear of muscle tissue for the last two inches of its course, and is inserted, when there is one, into the indentation of the outer margin of the patella.

ABERDEEN UNIVERSITY ANATOMICAL ANTHROPO- LOGICAL SOCIETY.

THE Society held five meetings in the months of June and November 1901 and January and February 1902.

At the meeting on June 1st the constitution of the Society was revised, and new rules framed and adopted.

The abnormalities found in the Practical Anatomy rooms during the present year were exhibited. They consisted of abnormal muscular slips, ossifications in tendons, and variations in the course and distribution of arteries and nerves.

Dr SLESSOR exhibited also a dissection in which the parotid salivary gland was absent on both sides, the only representative being an aggregation of glandular tissue about the size of a small almond in the buccal fossa on the one side and on the surface of the masseter on the other.

Miss MARGARET DUNCAN described the anatomy of a double chick embryo of 48 hours, with illustrative drawings and lantern slides, the actual sections being shown under the microscope.

Dr ALEX. LOW showed a specimen of transposition of the sigmoid flexure to the right side, terminating in the rectum over the right sacro-iliac synchondrosis. Two photographs were shown of the dissection.

On June 29th the annual business meeting of the Society was held, when the Office-bearers for the year 1901-1902 were elected as follows: *President*—Professor R. W. Reid, M.D., F.R.C.S. Eng. *Vice-Presidents*—Alex. Low, M.A., M.B., C.M.; Robert Aird, M.A., M.B., Ch.B.; C. T. Andrew, B.Sc. *Secretary*—James Clark. *Recording Secretary*—B. R. G. Russell. *Treasurer*—G. G. MacDonald, M.A.

At the meeting in November Miss ANNE MERCER WATSON, L.R.C.P. & S., read a paper entitled "Notes on Petrie's New Race," giving the result of a minute examination of skulls and other parts of skeletons found at El Amrah, in Upper Egypt, by Mr Randall-MacIver, and presented to the Anatomical Museum by Professor Reid. These specimens are believed to be at least 7000 years old, and were affirmed by Miss Watson to belong to at least 160 bodies. The skulls were those of middle-aged persons, with the exception of two which were those of old persons. Out of 25 skulls examined, 6 showed a capacity of between 1100 and 1200 c.c., 15 between 1200 and 1400, 3 between 1400 and 1500, and only one over 1500; thus 19 were microcephalic, 5 were mesocephalic, while only one was megacephalic.

Out of 42 skulls examined, 38 were dolichocephalic, 4 were mesaticephalic, while no brachycephalic ones were found. The

alveolar index calculated in 21 cases showed not a single case of prognathism ; 7 crania were mesognathous, and 14 orthognathous, the average index being 915.

The nasal index examined in 22 cases showed 7 crania to be platyrrhine, 8 to be mesorrhine, and 7 leptorrhine, the average index being 510. The orbital index in 22 cases showed 7 crania to be microseme, 11 mesoseme, and 4 megaseme, the average index being 833.6.

Thus the race had long heads of small cranial capacity, with no negroid prominence of the jaw. The orbits were square, and the noses broad across the bridge, but some wide and some narrow at the anterior nasal aperture.

Miss Watson went on to describe the vertebræ, on which were noticed rheumatic exostoses, a fact of some interest, as it is said rheumatism was unknown to the Egyptians.*

From the length of the bones of the appendages, it was inferred that the average height of the individuals to whom the bones belonged would be 5 feet 3 inches, and the tallest individual about 5 feet 11 inches. Numerous united fractures were found ; and it was noticed that of those of the forearm, 62 per cent. were of the shaft of the ulna in its lower third, while at the present day fracture of the ulna alone is very rare. To explain this, the view was brought forward that the race were slaves, and that when beaten by their taskmasters, they raised their arms to protect their heads, and in this way the ulna was injured.

Miss Watson then went on to discuss the origin of the 'New Race,' and concluded that they were a mixed one formed by Semitic and Libyan tribes, with a far-off strain of Negroes. The paper was illustrated by lantern views of the actual specimens.

At the January meeting, the abnormalities found in the Practical Anatomy rooms during the first half of the winter session were described. These abnormalities, which numbered fifteen in all, consisted of variations in connection with arteries, viscera, muscular slips, and bones. One specially interesting variation, from a developmental point of view, was that of the origin of the right subclavian artery from the dorsal aorta. The variations were demonstrated by those who had discovered them in the course of their work in the dissecting-room.

Notes were also read on observations made with regard to the relations of the palmar arches to the skin folds of the palm.

At the meeting in February, Mr B. R. G. RUSSELL read a paper on the Antiquities of Orkney. Mr Russell detailed the history of the Orkneys, describing the houses, towers or brochs, and burial mounds

. Rheumatoid Arthritis is by no means rare in modern Egypt, and its effects are very common in Egyptian skeletons. In the Cambridge Museum there are portions of about 280 vertebral columns which show traces of this disease.

of the Picts, and dealt in turn with the Norse period and the period under British rule. Some very fine specimens of stone implements of the Pictish period were exhibited; and the skull of a child under six years found in a stone cyst in Orkney was also shown. Mr Russell discussed the origin of the Picts, and mentioned that the view at present held was that they were the descendants of a race inhabiting Mid-Europe before the Teutonic invasion.

Mr IRVINE-FORTESCUE showed a Pictish idol found in Orkney, and mentioned that similar images had recently been unearthed at Troy, and this he believed to be a point in favour of the Phœnician origin of the Picts.

Lantern views were shown of various antiquities of Orkney.

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PROCEEDINGS OF THE
ANATOMICAL SOCIETY OF GREAT BRITAIN
AND IRELAND.

JULY 1901.

THE Summer Meeting of the Anatomical Society of Great Britain and Ireland was held in the Medical Department of the Yorkshire College, Leeds, on Friday, 5th, and Saturday, 6th July 1901. The President, Professor A. H. YOUNG, occupied the chair. On Friday the meeting commenced at 3 P.M. and lasted until 5.30. Twenty members and twenty-one visitors were present. On Saturday business commenced at 10 A.M. and was finished at 12.30. Eighteen members and twenty-four visitors were present.

The minutes of last meeting were read and confirmed.

The following were elected members of the Society:—E. J. JENKINS, M.B., C.M. (Edin.), Demonstrator of Anatomy, King's College, London, W.C., proposed by Arthur Robinson, A. H. Young, P. Thompson; H. H. BROOME, M.B., Demonstrator of Anatomy, The Owens College, Manchester, proposed by Alfred H. Young, Peter Thompson, Arthur Robinson.

THE PRESIDENT, before commencing the business of the meeting, said he had just learned that Professor His, an honorary member of the Society, was on the eve of his seventieth birthday, and suggested that the occasion should be utilised by the Society to present its congratulations to the veteran anatomist.

Professor G. D. THANE moved:—

“That the hearty and cordial congratulations of the Anatomical Society of Great Britain and Ireland be forwarded to Herr Geheimrath Professor Wilhelm His, on the occasion of his seventieth birth-

day, together with an expression of personal regard and esteem, and with every good wish for his future health and happiness."

Professor F. DIXON, a former pupil of Professor HIS, seconded the motion, which was unanimously adopted, the President being requested to transmit the same to Professor HIS.

The following communications were made:—

(1) Dr J. K. JAMIESON, *Dissection to show the Normal Origin of the Peroneus Tertius*.—Examination of 45 bodies showed that this muscle in 29 cases took origin from the anterior part of the internal surface of the shaft of the fibula, extending from a point $\frac{1}{2}$ to 2 inches above the middle of the shaft to within an inch of the external malleolus. In 6 cases the origin reached as far as the middle of the shaft; in 9 cases it arose from only the lower third. It was absent in 1 case only. The muscle extends upwards beyond its bony origin for a variable distance (1–2 inches), taking origin from the anterior peroneal septum, and downwards for about an inch, arising from the interosseous membrane, these fibres being usually closely associated with the extensor longus hallucis. The separation of the fibres of the peroneus tertius from those of the extensor longus digitorum is artificial, but very easy. There is no reason why it should not be described as part of the extensor longus digitorum, but when described separately, its origin is usually understated.

(2) Dr J. K. JAMIESON, *Pseudo-Meckel's Diverticulum*. — The lower part of the ileum of a male subject, aged 58, showed (1) a typical Meckel's diverticulum, 45 mm. in length, situated 29 inches from the ileo-cæcal junction; (2) a second diverticulum 10 inches higher up, situated on what may be called the inferior aspect of the gut, nearer the free border than the mesenteric. It closely resembles Meckel's diverticulum, is 36 mm. in length, 20 mm. in diameter at its base, and gradually tapers to a blunt extremity of about 10 mm. in diameter.

Its wall is somewhat thinner than that of the intestine, and is composed of an external serous coat; a middle muscular coat, mainly continuous, with the circular coat of the intestine, but has some longitudinal fibres prolonged into it; an internal coat, indefinite in character, composed largely of fibrous tissue, with an epithelial lining in patches and showing no crypts.

Across the orifice of the diverticulum there is a band of mucous membrane about 6 mm. broad.

There was no evidence of disease in any part of the alimentary canal.

The specimen was shown because, although most likely of the nature of a hernial protrusion, it is entirely unlike the ordinary hernial protrusions met with.

(3) Dr J. K. JAMIESON.—*Exhibition of brain dissections used*

for teaching purposes in the anatomical department; hardened in formalin, $7\frac{1}{2}$ per cent. solution, and preserved in a 1 per cent. solution.

(4) Dr J. K. JAMIESON.—An exhibit of a series of *Thyroid Glands* to show the form, and especially the pyramid and levator glandulæ thyroideæ. Thirteen specimens were examined for the series. The pyramid was found in 7 and the levator in 2. In one case the levator is small and connected with the thyro-hyoid muscle. In the other it is large: 30 mm. long and 9 broad, and entirely unconnected with any other muscle.

(5) Professor TREVELYAN (introduced by Professor GRIFFITH) described in detail a method which he employed for the *preparation of dry brain specimens*. He showed specimens so prepared which had been in use for years.

(6) Mr F. G. PARSONS showed a specimen of the Grison (*Galictis vittata*), in which the superior intercostal artery passed back (caudalward) through a series of *foramina in the transverse processes* of the anterior 5 thoracic vertebræ. The macerated thoracic vertebra of a polecat (*Mustela putorius*) was also shown, and it was seen that the segmental intercostal artery rose from the superior intercostal in the foramen, and emerged into the intercostal space through a small opening in the ventral bar of the arterial canal. Mr Parsons said that he had seen the same canal in the weasel and ferret, and suspected that it might be a characteristic feature of the family of the Mustelidæ among the Carnivora. The specimen is of some little interest to human anatomists owing to the fact that in 1883 Professor Sir William Turner¹ described a first thoracic vertebra of man with a perforation through the base of the transverse process. These and various anomalies of the cervical vertebræ made Mr Parsons suspect that three elementary processes, with two intervals or foramina between them, would eventually be recognised on the side of a typical generalised vertebra, and that the most ventral of these would correspond to the rib.

(7) *Dorsal Distribution of Median Nerve*.—Mr PARSONS showed a specimen of a Phalanger (*Phalangista vulpina*) in which a branch of the median nerve passed round the outer side of the forearm with a branch of the median artery, and supplied the part of the dorsum of the hand, which is usually supplied by the radial nerve. He had seen the same arrangement in several kangaroos, but it was not present in two bandicoots he had dissected. In those cases in which it occurs, the musculo-spiral nerve ends as the posterior interosseous, but no communication between the musculo-spiral and median exists in the upper part of the arm. The arrangement is an exaggeration of the human supply of the median to the dorsum of the terminal phalanges.

¹ *Journ. of Anat. and Physiol.*, vol. xvii. p. 255.

(8) Dr J. K. JAMIESON, *Diverticulum of the Pericardium*.—The diverticulum was found in the mass of fat lying between the pericardium and left pleura, behind the apex of the heart. Opening the pericardium, the orifice of communication with the pericardial cavity was seen on tilting up the apex of the heart. This orifice is 7 mm. in diameter, admitting an ordinary lead pencil. The sac gradually increases in size for a distance of 4 c.c., where its diameter is 24 mm., and then gradually decreases, ending in a blunt extremity. The length is 7 c.c. Its capacity is 3 fluid drachms. Its outer surface is rough, having the fatty tissue adherent to it. Its wall is directly continuous with the fibrous pericardium, and its interior is lined by serous pericardium.

There was no sign of disease in either heart or pericardium. The subject was a male, aged 61.

(9) Professor THANE exhibited and explained, on behalf of Dr D. NABARRO, organs from a child of fourteen weeks, showing *transposition of stomach and duodenum, absence of hepatic section of inferior vena cava, supplementary lobe of liver, absence of spleen, malformation of heart, viz., occlusion of left auriculo-ventricular aperture, persistence of interventricular foramen, common origin of aorta and pulmonary artery*. The case is fully described in the October number of the *Journal of Anatomy and Physiology*.

(10) Professor WARDROP GRIFFITH exhibited a series of specimens showing *abnormalities of the heart*.

(11) Mr J. H. WATSON gave a lantern demonstration showing *the origin and nature of the hydatiform bodies in the testicle and broad ligament, and the fate of the Müllerian duct in the Epididymis*.

This communication will be published in full in the *Journal of Anatomy and Physiology* for January 1902.

(12) Mr H. SECKER WALKER (introduced by Professor GRIFFITH) showed a beautiful series of specimens illustrating the *age changes and surgical anatomy of the temporal bone*.

(13) Professor ARTHUR THOMSON gave a lantern demonstration on *the form of the lower epiphyseal suture of the femur in various classes of mammals*. This communication will appear in the *Journal of Anatomy and Physiology* for January 1902.

(14) Professor PATERSON made a communication on *the morphology of the sternum*, in which he argued that the sternum is essentially median, independent, and unsegmented, and that the comparative anatomy, development, and structure of the bone indicate its independence in the first instance of costal elements, and its genetic association with the shoulder girdle.

(15) Dr WAKELIN BARRATT gave a lantern demonstration on *the form and position of the cerebral ventricles*. This communication will be published in full in a later number of the *Journal of Anatomy and Physiology*.

(16) Professor A. FRANCIS DIXON showed some specimens illustrating *a method of preparing the hollow viscera for demonstration purposes by impregnating their walls with gelatin and then treating them with formalin*. Details of the method will appear in the *Journal of Anatomy and Physiology*.

(17) Professor A. FRANCIS DIXON exhibited models of *sections of the male and female pelvis prepared from specimens hardened with formalin*, and also *models of the bladder in varying degrees of distension*. Illustrations, prepared from two of these models, will be found in a joint paper *on the peritoneum of the pelvis*, by Professors Birmingham and Dixon, in the *Journal of Anatomy and Physiology*.

PROCEEDINGS OF THE
ANATOMICAL SOCIETY OF GREAT BRITAIN
AND IRELAND.

NOVEMBER 1901.

THE Annual General Meeting of the Society was held on Friday, November 29th, in the Middlesex Hospital Medical School, at 4 P.M. The President, Professor A. H. YOUNG, was in the chair, and twelve members and twenty-three visitors were present. Letters regretting their inability to attend were received from Professor B. C. A. WINDLE and Professor ARTHUR THOMSON.

The minutes of the last meeting were read and confirmed.

The following officers for the ensuing year were then elected:—
President—C. B. Lockwood. *Vice-Presidents*—R. Clement Lucas, M.S.; Arthur Thomson, M.B.; A. M. Paterson, M.D. *Treasurer*—G. B. Howes, LL.D., F.R.S. *Secretaries*—Peter Thompson, M.D. (England); T. H. Bryce, M.D., F.R.S.E. (Scotland); Ch. Patten, M.D. (Ireland). *Council*—C. Addison, M.D.; R. J. Berry, M.D., F.R.S.E.; A. Birmingham, M.D.; J. Black, M.B.; D. J. Cunningham, M.D., F.R.S.; A. F. Dixon, M.B.; E. Fawcett, M.B.; W. H. Gaskell, M.D., F.R.S.; Robert Howden, M.B.; A. Keith, M.D.; A. Macalister, M.D., F.R.S.; J. Musgrove, M.D.; F. G. Parsons; W. G. Ridewood, D.Sc.; Arthur Robinson, M.D.; Barclay Smith, M.D.; J. Symington, M.D.; G. D. Thane; A. H. Young, M.B.; B. C. A. Windle, M.D., F.R.S.

Votes of thanks were passed to the retiring President, Professor A. H. YOUNG, and the retiring Secretary for England, Dr ARTHUR KEITH.

The Treasurer's report, showing a balance of £42, 8s., was received and adopted.

In presenting his annual report, Professor G. B. Howes stated that during the year there had been six resignations, and that the number of members on the Society's roll had reached 156. He remarked that the feature of the past year had been the large recovery of subscriptions in arrear, the amount received from that source having been but once before exceeded. The amount received in current subscriptions fell short of the year's expenditure by more than 35 per cent., but that, assuming full payment during the ensuing year, the financial position of the Society was assured.

Regret was expressed at the loss by resignation of Professor Sherrington, F.R.S.; and the Hon. Treasurer paid a passing tribute to the memory of Dr W. Anderson and Professor A. W. Hughes, deceased.

(1) *Diagrams illustrating the Arrangement of the Hair on the Frontal Region of Man.* By WALTER KIDD, M.D., F.Z.S.

This series of diagrams has been prepared for the purpose of illustrating the arrangement of hair on two portions of the frontal region in man, on the general principle that the smallest phenomena of Nature are worthy of a measure of investigation, and most of them capable of interpretation. It is unnecessary to prove that these are truly phenomena of nature, for the cases from which they are taken ranged from the age of a few hours to six years, and the operation of secondary causes has been eliminated in all of them. To use the expression of Galton, they are products of nature rather than nurture in the individuals, and, I submit, of nurture rather than nature in their ancestors.

These observations relate to two borders of the frontal region, that found at the edge of the scalp, and that which lies at the level of the eyebrows, and these two situations have been chosen for examination because they are specially open to the incidence of certain mechanical forces. The figures nearly explain themselves, and are intended to show the chief situations in which the hair-streams from the scalp are parted, and the ways in which they are arranged before being lost in the surrounding streams of the frontal region.

At the border of the scalp the chief point of interest as to the direction taken by the hair coming from the vertex is the difference between the modes in which it is parted. The main direction of hair on the frontal region between the scalp and the eyebrows is towards the temporal region, and it takes a sharp curve at the upper border downwards and to the temporal region, and at the lower border upwards and in a similar direction. On account of the convex outline of that portion of the cranium where the scalp ceases, the hair-streams here must part in one way or another. But it is noteworthy that the ways in which they do part group themselves into three leading arrangements, the most frequent of which is that the parting is on

the left side of the middle line. This parting may also be found to the right of and in the middle line, and certain other rare arrangements are found, some of which are noted in the diagrams. Even at the risk of repetition, it needs to be pointed out that the partings referred to are only those found at the border of the scalp, and are sometimes indefinite, being merely the situations where the streams of the scalp divide and pass to left and right.

Fig. 1 shows the direction of hair to be entirely downwards, and such partings as exist are central.

Fig. 2. Here all the direction is also downwards, except for a very singular reversed feathering of the hair to the right of the middle line, representing a right lateral parting.

Fig. 3. In this case the direction is all upwards from the frontal region, and the hair here meets that of the scalp and radiates from the middle line upwards and outwards.

Fig. 4. Direction downward in central stream, with two lateral upward streams.

Fig. 5. This is far the commonest arrangement, the direction being all downwards, with parting to the left of the middle line.

Fig. 6. Here the parting is on the right of the middle line. In the majority of cases the direction is downward, and more rarely upwards.

Fig. 7. Rare and singular form seen only in very young infants, with V-shaped arrangement, the borders of which are upturned. This arrangement in a young subject has a most suggestive resemblance to the triangular area seen on the forehead of a bald adult, formed by the junction of the two frontal portions of the occipito-frontalis muscle when in strong action; the latter occupies exactly the situation of the former, suggesting that constant muscular action causes the curious hair arrangement which is inherited in a few cases.

Fig. 8. Direction downwards, left lateral parting, with perceptible continuation over the frontal region as far as the eyebrow.

Out of 70 cases, examined specially for this purpose, 45 showed the left lateral, 17 central, 6 right lateral parting, and 2 the curious V-shaped arrangement indicated.

The inference which one would draw from these facts of hair-direction, doubtless not very numerous, but representative of a very large number of cases not so carefully examined, is that probably most of them, certainly some, are produced in the individual by inherited effects of dressing the hair in ancestors. The frequency of the central and left and right lateral partings, and the great preponderance in numbers of the left lateral, are very suggestive of the three common methods of dividing the hair in this region. Whatever significance they possess, they do not point to inheritance from a simian ancestry, being entirely unrepresented in anthropoid apes or monkeys, except in the case of the central parting of a chimpanzee. In most of these animals the hair on the frontal region passes from the superciliary region right over the low forehead and backwards over the vault of the cranium in one uniform stream.

The second portion of the frontal area referred to here is that

which lies at the level of the eyebrows. A very singular and well marked break in the stream forming the eyebrows is seen in all hairy subjects, and lies always over the spot where the outer attachment of the corrugator supercilii draws in the skin in knitting of the brows. This break in the stream would appear to be caused by the traction of the underlying muscles on the skin, rather than by any adaptation of the hair to the shape of the superciliary ridge. Figs. *a.*, *b.* also show the commonest situation of the two lateral vertical wrinkles caused by the action of the corrugator supercilii, also the rare central wrinkle.

The direction of hair indicated in the figure where the streams of the two sides frequently decussate across the middle line is probably due to the constant action of the corrugator supercilii. Whether these small phenomena at the level of the eyebrows be produced as suggested or not, the arrangement is at least singular, and unlike that found in apes and monkeys. In considering the facts of hair-direction on the human body, it is necessary to bear in mind that some of the most suggestive of these are fugitive in character, some being only observable in infants for a few months, and then being obliterated for the rest of life; others are more manifest at about the age of puberty in a hairy subject. But, from the point of view of inheritance, they must possess a measure of significance, whatever be the age at which they occur, and however fugitive their character.

DESCRIPTION OF PLATE.

Fig. 1. Downward direction, with indefinite central parting—J. B., at 5 years old.

Fig. 2. Central and lateral streams downward, with upward feathering on the right.—B. B. at 2½ years old.

Fig. 3. Upward direction, lower border indefinite.—H. J. K. at 3 months, and B. R. at 11 weeks.

Fig. 4. Central stream downward, lateral streams upward.—J. M. at 3 years old.

Fig. 5. Downward direction, with left parting.—B. W. at 6 hours old.

Fig. 6. Upward direction, with right parting.—W. G. at 6 years old.

Fig. 7. V-shaped area, downward direction, with upturned borders.—B. R. and B. W. at 6 weeks.

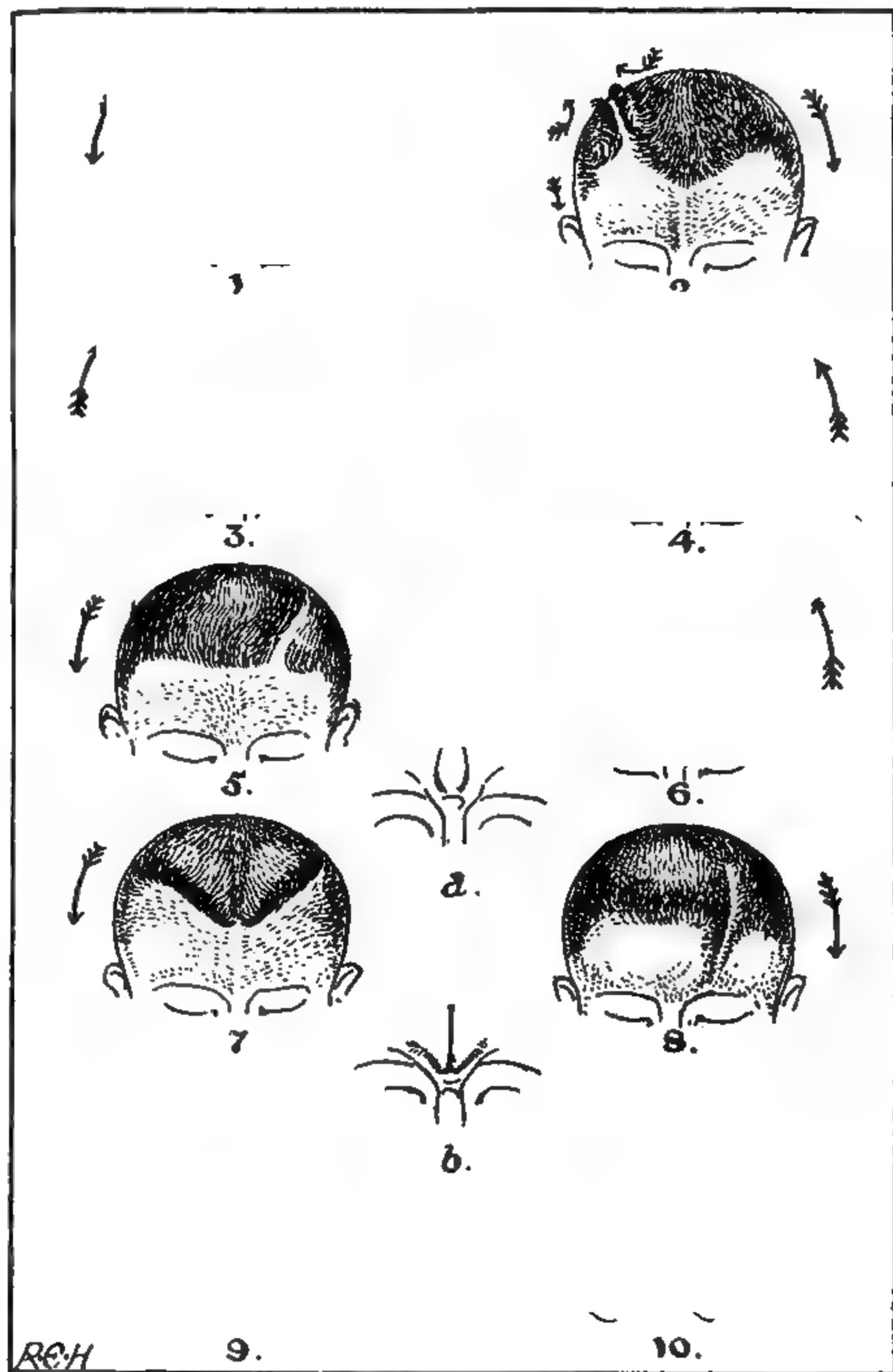
Fig. 8. Downward direction, with left lateral parting continued over forehead.—B. B. M. at 4 days old.

Fig. 9. Superficial muscles of frontal region and orbit.

Fig. 10. Arrangement of hair of eyebrows in a very hairy subject.

a. Commoner bilateral vertical wrinkle in middle portion of frontal region.

b. Central vertical wrinkle in frontal region—less common.



(2) *A Note on the Development of the Fundus of the Human Stomach.* By ARTHUR KEITH and F. WOOD JONES.

The object of this communication was to show that the fundus of the human stomach—that part which lies to the left of a line prolonging the axis of the abdominal part of the œsophagus—is developed, not as a general expansion of the gastric part of the fore gut, but in the form of a localised outgrowth or diverticulum from the cardiac end of the greater curvature (dorsal border) of the stomach, and in its manner of origin had much in common with the process which springs from the hind loop of the gut, and gives rise to

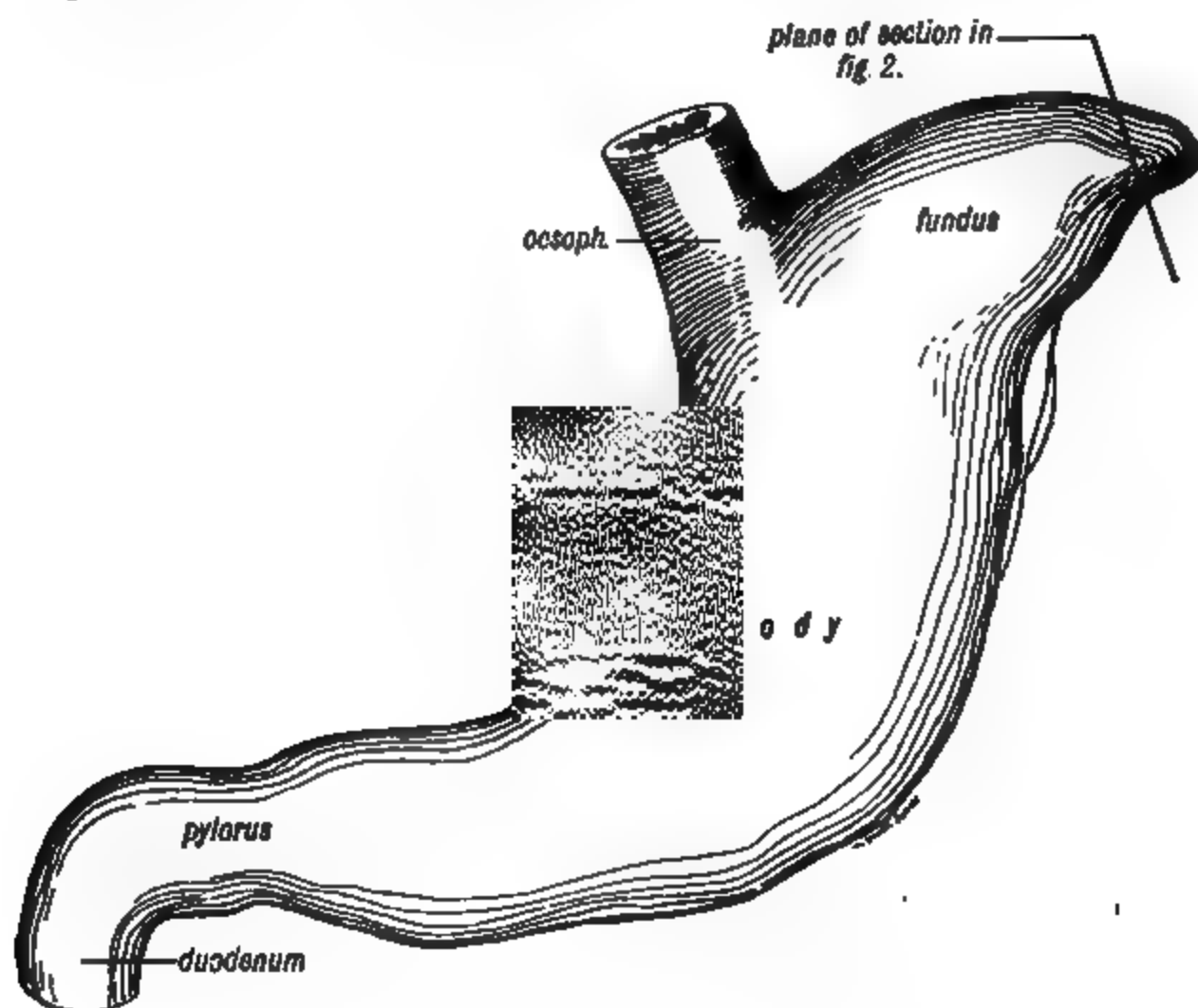


FIG. 1.—Profile of the human fetal stomach at the end of the third month, showing the fundal process—(F. W. Jones).

the cæcum and appendix vermiformis (fig. 1). The process is best marked in human fetuses in the third and fourth months of development; after these months the diverticulum of the fundus is less distinctly demarcated, becoming expanded, and merged with the body of the stomach. The apex of the outgrowth, which is usually conical in shape, and directed against the left dome of the diaphragm, arises chiefly from the left side of the dorsal mesogastrium (gastrophrenic ligament and gastrosplenic omentum), the attachment of which is thus thrust to the right (posterior) aspect of the fundus.

The manner in which the fundus is developed helps to explain the peculiar arrangement of its muscular coats. Recently Professor Birmingham, in a paper contributed to the *Journal of Anatomy and Physiology*, vol. xxxiii. p. 22, showed that the muscular fibres of the middle or circular coat which surround the body and pyloric part of the stomach are drawn obliquely toward and become lost on the fundus, while the fibres of the internal coat are practically confined to

FIG. 2.—Section across the apex of the fundal outgrowth of the stomach of a fetus at the end of the third month. The position of the section is shown in fig. 1—(F. W. Jones).

the fundus, and are arranged in a circular manner round it, the central whorls commencing at the apex of the outgrowth.

Originally the authors were inclined to regard the vasa brevia from the splenic artery as the vessels of the fundus, but further observation showed them that the part of the stomach which arises from the localised outgrowth was supplied by the upper two vasa brevia and from the coronary artery.

A transverse section of the diverticular outgrowth of the fundus (fig. 2) at the end of the third month shows four distinctly marked strata in its walls. Of these four strata, the most outstanding is the submucous; it is extremely thick and cellular, furrowed and ridged, the ridges commencing in the apex of the outgrowth, and radiating towards the body of the stomach. The inner or mucous stratum is extremely simple; it covers the ridges and furrows; the epithelial cells are cubical, with large oval nuclei situated centrally; the mucous membrane shows a closely packed and uniform series of tubular depressions, each depression being from six to eight cells deep. The muscular stratum consists almost entirely of muscular cells arranged in a circular direction on the outgrowth; there is then no certain evidence of a longitudinal coat, although this can be detected in the terminal part of the œsophagus and towards the pyloric end of the stomach. The outer stratum is the serous, with subserous cellular tissue. In the fourth month, outgrowths from the thick submucous stratum spread between the tubular depressions of the mucous coat in the form of needle-like cellular processes.

Longitudinal sections of the stomachs of fœtuses in the fourth month of development showed certain peculiar characters in the gastric mucous membrane. While the mucous membrane of the terminal part of the œsophagus and the body of the stomach showed the same form of cells and of tubular depressions as have just been described in the fundus, the pyloric part of the stomach (the part which afterwards forms the antrum pylori and pyloric canal) showed a mucous coat which, in the character of its cells and glandular depressions, resembled that within the first stage of the duodenum. In the pyloric part of the stomach the glandular depressions are wide and deep, the folds or processes between the depressions having the characters of villi, which have been already described by Toldt in the human fœtal stomach. The cells of the mucous membrane of the pyloric part of the stomach, like those of the duodenum, are columnar; the oval nuclei are situated towards the bases of the cells; the upper parts of the cells are clear, sharply demarcated from each other, and apparently contain a mucoid material. The cells of the cardiac part of the stomach, on the other hand, are cuboidal, granular, with central nuclei. While the pyloric glands are deep and well marked, the cardiac are shallow depressions. It will be thus seen that during the fourth month the mucous membrane of the pyloric part of stomach, in its villous appearance, in the shape of its glands and characters of its epithelium, agrees much more closely with the duodenum than with that of the cardiac part.

The tripartite nature of the stomach of Primates.—The stomach of *Semnopithecus*, an ape found in the East, from India to Borneo, and undoubtedly one of the most ancient and primitive simian types now extant, has always been a puzzle to zoologists. Its stomach has a striking superficial resemblance to that of the sheep (fig. 3). It consists of three sharply differentiated and highly specialised compartments, which are already demarcated before birth. It was to see if any light could be thrown on the nature of the stomach of *Semno-*

pithecus that induced the authors to investigate the stomach in human fetuses. They also found, from numerous observations made by one of them, that it was not uncommon to find in the stomach of the anthropoids, and also to a lesser degree in that of the apes (especially so in *Mycetes*), clear indications of three chambers, viz., a fundus, a body, and a pyloric part (made up of the antrum pylori and the pyloric canal). Addison's observations on the position of the abdominal viscera, made accurately, but without special reference to the demarcation of the stomach into compartments, show that the fundus is more or less clearly marked off by a constriction from the

FIG. 3.—The stomach of *Semnopithecus*—(F. W. Jones).

body of the stomach in a large proportion of cases. The authors conclude, therefore, from the evidence of development and of comparative anatomy, that the stomach of the Primates (excluding the Lemuroidea) is probably tripartite in nature, consisting of a fundus, a body, and pyloric part. In *Semnopithecus*, and, to a certain extent, in *Mycetes*, each of these three parts has become highly specialised. They regard the diverticular outgrowth for the fundus as the representative of the first stomach of *Semnopithecus*.

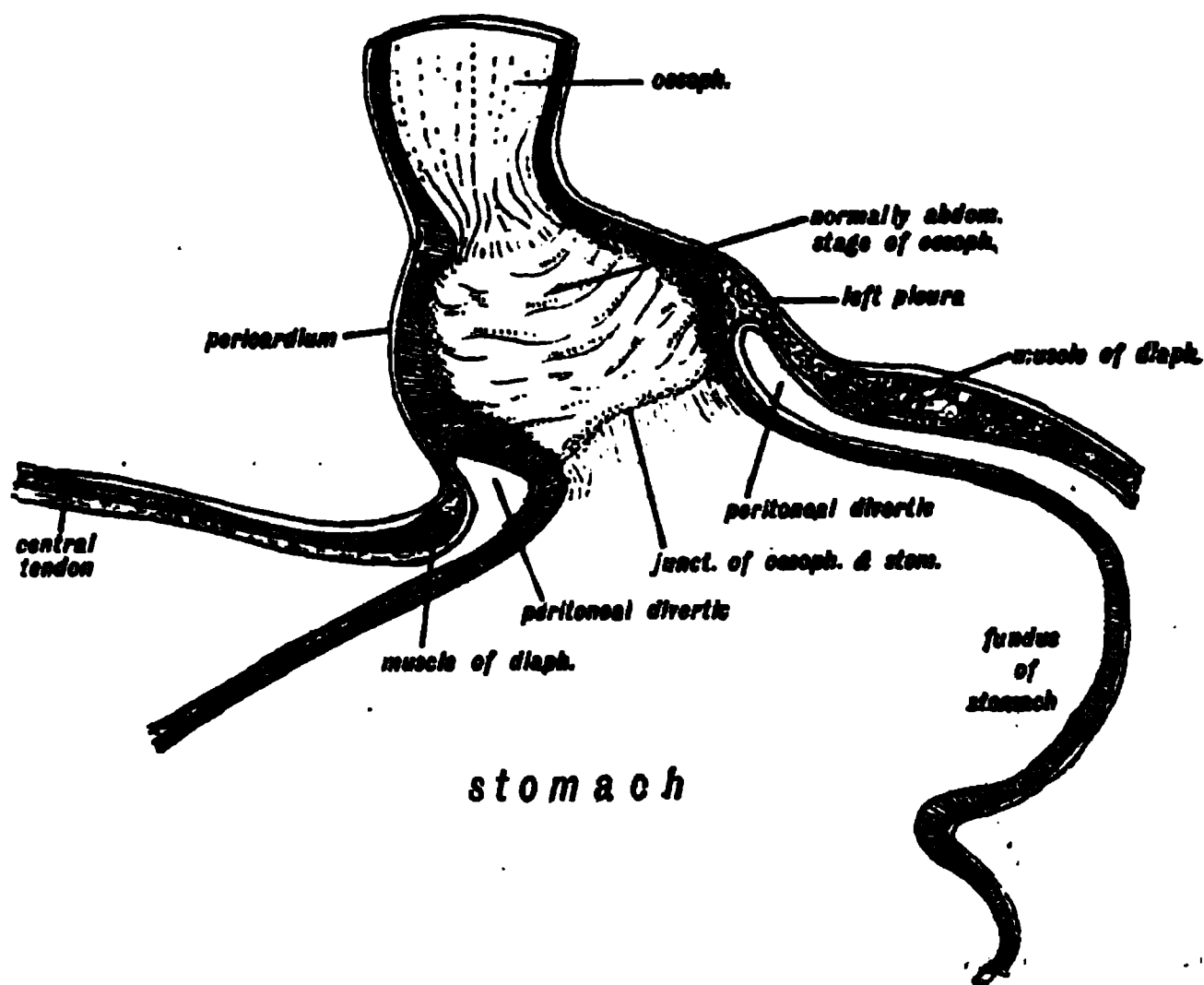
The two ridges seen (fig. 3) running from the opening of the oesophagus to the second compartment of the stomach of *Semnopithecus*, along the lesser curvature, may meet so as to enclose a tubular canal, probably for the conveyance of fluids. Such a groove,

with vestigial ridges, can certainly be detected in the human foetal stomach. The mucous membrane of the first and second compartments of the stomach of *Semnopithecus* are of similar structure, the first having the more abundant supply of lymphoid tissue.

It may be of interest to mention that the diet of *Semnopithecus* consists mainly of bamboo shoots and leaves, to a lesser extent of fruit, and that although the adult animal (contents of stomach included) weighs only from thirteen to fifteen pounds, the contents of its stomach weigh from three to five pounds. That is to say, if an average man were to feed at a similar ratio as regards weight, he would require to eat a dinner weighing from thirty to forty pounds.

(3) *Complete absence of the Right Lung, Bronchus, and Pulmonary Vessels in a recently born child.*—This specimen was shown for Dr FINDLAYSON by Mr F. W. JONES. The left lung was hypertrophied, pushing the heart over to the right side of the thorax; the right lung was completely absent. The trachea ended in the left bronchus, it being impossible to say where the one began and the other ended. The right pulmonary veins and artery were undeveloped. The left auricle and appendix were smaller than normal. The child lived for some hours after birth.

(4) *A partial Hernia of the Cardiac End of the Stomach through the œsophageal orifice of the diaphragm.*—The specimen was shown, in the absence of Mr RIGBY, by Mr F. W. JONES. It was removed, after the parts had been examined *in situ*, from a dissecting-room subject, a female over 60 years of age, but of whom no clinical history could be obtained.



Section through the stomach, œsophagus and diaphragm of Mr Rigby's case—(A. K.).

The œsophageal orifice of the diaphragm measured 5·6 cm. in diameter; the muscular band which surrounded the left side of the orifice was highly developed, that on its left side was less so. The stage of the œsophagus which lies normally within the abdomen was dilated, drawn within the posterior mediastinum behind the pericardium, and covered on its left and anterior aspects by the left pleura (fig. 4). The line demarcating the œsophageal from the gastric mucous membrane lay above the level of the diaphragm, part of the cardiac end of the stomach filling the œsophageal orifice. A circular fold of peritoneum was also drawn through the orifice with the cardiac part of the stomach (see fig. 4).

Since the above case was exhibited, another female subject (aged 65) in the dissecting-room of the London Hospital showed the same condition, only in a more marked degree. A diverticulum representing a third of the cardiac part of the stomach lay above the diaphragm. It might have been mistaken for a case of dilatation of the œsophagus had a careful examination not been made.

Mr KEITH regarded the abnormal condition as being due to the manner in which the fundus of the stomach was developed, but the consensus of opinion among the members present was that the condition was pathological, and due to a dilatation of the œsophagus.

(5) Dr R. J. GLADSTONE showed some *cephalometric instruments*.

1. An improved form of callipers designed by Mr J. Gray, for

recording the maximum longitudinal and transverse diameters of the head.

FIG. 2

A full account of this instrument will be found in the *Journal of the Anthropological Institute*, vol. xxxi, 1901, p. 111.

2. An instrument (fig. 1) for measuring the distance between the biauricular line and bregma. The ear-plugs move in a horizontal

plane. The measurement is thus unaffected by differences in the transverse diameter of the head, as is the case with the calliper form of instrument in which the ear-plugs move in the arc of a circle.

3. A machine (fig. 2) for drawing the contour of the head. This is taken in a horizontal plane passing through a spot just above the glabella in front, and through the occipital point behind. The exact contour is recorded by means of a pencil which moves upon a sheet of paper placed a short distance above the head of the individual.

Dr Gladstone also showed some cephalograms taken with this instrument, illustrating different types of contour.

(6) Dr F. H. THIBLE gave a demonstration of a heart showing complete transposition of the aorta and pulmonary artery, with complete separation of the right and left ventricles. A detailed account of the preparation will appear subsequently.

FEBRUARY 1902.

A MEETING of the Anatomical Society of Great Britain and Ireland was held in the St George's Hospital on Friday, February 14th, at 4.30 P.M. The President, Mr C. B. LOCKWOOD, occupied the chair, and sixteen members and six visitors were present.

The minutes of the last meeting were read and confirmed.

The following candidates were elected members of the Society :—
 JOSEPH GRIFFITHS, M.A., M.D., F.R.C.S., proposed by G. D. Thane, C. B. Lockwood, Peter Thompson. W. D. HARMER, M.A., M.B., F.R.C.S., Junior Demonstrator of Anatomy, St Bartholomew's Hospital Medical School, proposed by C. B. Lockwood, R. C. Bailey, Peter Thompson. J. K. MURPHY, M.A., M.D., F.R.C.S., Assistant Demonstrator of Anatomy, St Bartholomew's Hospital Medical School, proposed by C. B. Lockwood, R. C. Bailey, Peter Thompson. R. A. NEEDHAM, B.Sc., M.B., Junior Demonstrator of Anatomy, The Owens College, Manchester, proposed by A. H. Young, Peter Thompson, H. H. Broome. W. B. BILLINGHURST, B.A., proposed by Arthur Thomson, A. M. Paterson, A. Keith. H. M. FLETCHER, M.B., F.R.C.S., Senior Demonstrator of Anatomy, University College, Liverpool, proposed by A. M. Paterson, A. Keith, Arthur Thomson.

(1) Mr F. G. PARSONS showed some wooden models of abdominal and thoracic viscera, in which the different areas of contact with adjoining viscera were painted in different colours.

(2) *A very long Vermiform Appendix enclosed in a Canal behind the Cæcum and Ascending Colon.* By R. S. TREVOR, M.A., M.B. (Cantab.).

The unusually situated and very long vermiform appendix now described was found during the post-mortem examination of a man aged 34 years, of Belgian nationality, who died from general septic peritonitis, following acute ulcerative colitis with perforation.

An examination of the cæcal region failed at first sight to reveal the presence of any appendix at all. On handling the gut, however, a rounded cord could be felt on the posterior surface, commencing at the point of convergence of the anterior and interior longitudinal muscular bands, just below the ileo-colic junction, and running upwards behind the ascending colon. The cord could not be separated from the bowel, and appeared to be lying over the posterior longitudinal muscular band. The peritoneum covering the ascending colon was reflected from either side of it on to the posterior abdominal wall, so that the cord lay behind the peritoneum, between the layers of a very short meso-colon.

When the ascending colon had been separated from its attachments and the under surface exposed, a small wormlike process, which was curled upon itself, was seen projecting from the gut just below the hepatic flexure. This wormlike process proved to be the end of an elongated appendix, projecting from a firm fibrous canal, which, with the appendix inside it, formed the cord already described.

The upper end of the canal presented a definite edge and was open, save for some very delicate connective tissue, continued on to the projecting end of the appendix. The lower end was completely closed, and showed no indication of any opening.

After slitting open the canal from above downwards, the appendix, which was lying free within it, was lifted out, and was found to measure—when straightened out but not stretched—9½ inches.

To the naked eye the appendix appeared healthy; there was no sign of inflammation around its tip or in any part of its course.

The retro-peritoneal situation of the vermiform appendix is by no means unusual, but the presence of the fibrous sheath surrounding it is distinctly remarkable. It is also by no means rare for the appendix to be found lying pointing upwards within an ileo-colic or ileo-cæcal pouch, and in cases of closure of the lower opening of such a pouch the appearance of absence of an appendix, such as was noted in the present instance, would be found. In this instance, too, the lower end of the canal showed no sign of any such opening, while the upper end was unmistakably open. Within the canal there was no sign of any meso-appendix, as might have been the case had the canal been an ileo-cæcal pouch closed by adhesions.

In the *Journal of Anatomy and Physiology*, vol. xxiv. p. 20, Professor Fawcett mentions that the longest appendix he had met

Drawing showing the under surface of the cæcum and part of the ascending colon, with the vermiform appendix and part of the canal in which it lay. The canal has been laid open and pegged out with bristles. To the left is the ileum with a portion of its mesentery above. The upper portion of the ascending colon and part of the canal containing the appendix were unfortunately torn off after removal of the specimen.

with was 19 cm. or $7\frac{3}{8}$ inches, and that Ribbert had recorded one 21 cm. or $8\frac{3}{8}$ inches long. In *Quain's Anatomy*, vol. iii. part iv. p. 109, it is stated that Rausshoff has recorded one measuring 230 mm. or $9\frac{1}{8}$ inches. The length of the appendix I have described, viz. $9\frac{1}{2}$ inches, is therefore remarkable.

The drawing, for which I am indebted to Mr C. R. S. Bradley, Special Assistant House Officer, St George's Hospital, shows the under surface of the cæcum and part of the ascending colon, with the appendix, and part of the canal in which it lay. The appendix has been lifted out to show the canal, which has been pegged out with bristles. To the left is the lower end of the ileum, with a portion of the mesentery above it. From the point of attachment of the appendix, the anterior and interior longitudinal muscular bands of the colon are seen diverging.

(3) Dr TREVOR also showed a *Heart with various Malformations*.

The specimen was obtained at the autopsy on a child aged 9 years who died from pyæmia.

The heart is small, weighing 5 ozs. Both auricles and the left ventricle are well developed; the right ventricle is rudimentary.

On opening the right auricle, the foramen ovale is seen to be widely patent—the opening measuring 12 mm. in its transverse and 14 mm. in its vertical diameters respectively.

The inter-auricular septum posterior to the foramen ovale is also cribriform. The cavity of the auricle is traversed by two muscular threads, apparently continuations from the muscoli pectinati of the auricular appendix. The upper and longer of the two passes across the cavity from the appendix to just above the entrance of the inferior vena cava, the shorter one crosses the opening of the foramen ovale.

The right ventricle, which is extremely small, gives off a normal pulmonary artery with normal valves.

In the situation of the undefended space in the interventricular septum is an oval aperture measuring 17 mm. by 15 mm.—the direction of the longest diameter being from the base to the apex of the heart, and of the shortest at right angles to this in the plane of the septum.

The right auriculo-ventricular opening is guarded by a single flap formed by the fusion of the two outer segments of the tricuspid valve. This is attached above to the tricuspid ring and anterior margin of the opening in the septum, below by rudimentary chordæ to one rudimentary papillary muscle arising from the interventricular septum. The septal segment is wanting.

On opening the left ventricle, the two mitral segments are seen to be attached along their inner margins directly to the ventricular septum, one in front of and the other behind the opening already referred to. The outer margins are practically united to one another, whilst the free edges are joined by very short chordæ to two rudimentary papillary muscles, which are normally situated.

Owing to the direct attachment of the anterior mitral valve segment to the interventricular septum, sub-aortic stenosis is present.

A finger introduced from the left ventricle *between* the mitral valve curtains passes to the left into the left auricle, to the right through the deficiency in the interventricular septum into the right auricle above, and under the tricuspid valve into the right ventricle below. This last opening only admits the tip of the finger. In this way free communication exists between all four chambers of the heart.

The coronary arteries arise by a common trunk from the left posterior sinus of Valsalva.

Dr Trevor expressed his thanks to Dr F. G. Penrose for permission to show the specimen.

(4) Dr J. S. GOODALL gave a lantern demonstration on *The Comparative Histology of the Urethra*, in which he described the minute structure of the urethra in the following animals—

- Rodentia* (a) Myomorpha: i. *Mus musculus*; ii. *Mus decumanus*.
- (b) Hystricomorpha: *Cavia aperea*.
- (c) Lagomorpha: i. *Lepus timidus*; ii. *Lepus cuniculus*.
- (d) Sciuromorpha: *Sciurus vulgaris*.
- Carnivora*. *Felis domesticus*.
- Insectivora*. *Erinaceus Europæus*.
- Anthropoidea*.
- Ungulata*. *Ovis aries*.

The chief points dwelt on being—

(a) The nature of the epithelium. This differs considerably in different animals, and in the same species of animal at different times, but in all the animals examined (except the Lagomorpha) the epithelium was compound throughout, consisting of several layers of cells. In no case was the epithelium simple and columnar, as is often described.

(b) The muscle coat. This is usually described as consisting of an inner longitudinal and an outer circular layer; but although the arrangement of the muscle differs much in the above animals, often consisting of three distinct layers, yet in all cases the inner fibres are circular, and no distinct longitudinal layer could be made out.

(c) The sub-epithelial connective tissue. This is practically non-existent in all animals examined, the circular muscle appearing to support the epithelium directly, so that no muscularis mucosæ can be differentiated off from the general muscle coat.

A full account of Dr Goodall's communication will appear subsequently in the *Journal of Anatomy and Physiology*.

(5) Dr JOSEPH GRIFFITHS read a paper on the *Normal Position of the Great Toe*, illustrated by preparations and specimens. A full account of this communication will appear in the July number of the *Journal of Anatomy and Physiology*.

PROCEEDINGS OF THE
ANATOMICAL SOCIETY OF GREAT BRITAIN
AND IRELAND.

MAY 1902.

A MEETING of the Anatomical Society of Great Britain and Ireland was held at the Charing Cross Hospital Medical School on Friday, May 9th, at 4 p.m. The President, Mr C. B. Lockwood, occupied the chair, and fourteen members and four visitors were present.

The minutes of the last meeting were read and confirmed.

The following candidates were elected members of the Society :—
T. C. SAVAGE, M.B., B.S., F.R.C.S., University College, London, proposed by G. D. Thane, F. B. M. White, D. Armour. J. E. S. FRAZER, F.R.C.S., Demonstrator of Anatomy, St George's Hospital Medical School, proposed by F. Jaffrey, C. B. Lockwood, Peter Thompson. L. B. RAWLING, B.A., M.B., F.R.C.S., St Bartholomew's Hospital Medical School, proposed by W. Bruce Clarke, C. B. Lockwood, R. C. Bailey. E. CANNEY RYALL, F.R.C.S.I., Westminster Hospital, proposed by J. Black, A. Robinson, A. Keith. A. G. PITTS, Demonstrator of Anatomy, Charing Cross Hospital Medical School, proposed by C. Addison, C. B. Lockwood, Peter Thompson. F. W. JONES, London Hospital Medical College, proposed by A. Keith, H. Rigby, J. H. Watson.

The following communications were made :—

- (1) *Inflation of the Nasal Canal in the Skulls of Adult Gorillas and Chimpanzees, and the relative development of the Sinus Maxillaris and Inferior Meatus in Man and Apes.* By ARTHUR KEITH, M.D.

A skull of an adult male gorilla was shown in which the sinus maxillaris had been opened by the removal of its outer wall (see fig. 1). Within the sinus, and occupying nearly one-half of its entire capacity, was seen a globular expansion of the outer wall of the nasal canal. Some years ago, while examining the anthropoid skulls in the Collections of the British Museum and Royal College of Surgeons of England, he observed that such an expansion of the nasal canal was

present in the skulls of all adult gorillas and chimpanzees, both male and female, but was not present in either the orang or gibbon, nor in any other primate, at least in such a form as is seen in the gorilla and chimpanzee. The distension is more marked in the gorilla than in the chimpanzee.

The distension of the nasal canal in these two anthropoids begins about the time of the eruption of the second permanent molar tooth (about the 9th or 10th year). At first it seemed probable that the

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FIG. 1.—The skull of an adult Gorilla (male), with the outer wall of the maxillary sinus removed to show the inflation of the nasal duct within that cavity. Part of the nasal canal has also been cut away to show the inferior meatus.

distension affected not only the bony walls of the nasal canal, but also the nasal duct itself; but although an opportunity has not yet occurred of examining the condition of the nasal duct in an adult anthropoid, a study of younger animals and of other primates had shown that the distension, at its commencement, is properly one of the inferior meatus, and that the duct itself is not involved. Further, an extended investigation showed that the distension of the inferior meatus was a factor in the growth of the face in all lower primates, and that it was superseded to a greater or less extent by the develop-

ment of the maxillary sinus in the evolution of the anthropoids and man (see fig. 2).

Although the distension of the nasal canal within the maxillary sinus is not present to a marked degree in the gorilla and chimpanzee until the eruption of the second permanent molar, yet the commencement of this distension may be seen at the end of the eruption of the milk dentition as a small oœcal diverticulum of the mucous membrane of the inferior meatus, produced upwards behind the nasal duct, but within the bony wall of the nasal canal. Thus the inflation or distension which takes place in the higher anthropoids is really one of the inferior meatus.

In fig. 2 is shown the relative developments of the inferior meatus and maxillary sinus in a baboon approaching the end of the permanent

FIG. 2.—Lateral wall of the nasal cavity of *Cynocephalus babouin*, showing the large inferior meatus and small maxillary sinus.

dentition (7th year). It will be observed that the maxillary antrum is relatively small, and only distends that part of the jaw which lies over the last permanent molar; the inferior meatus distends that part of the jaw which lies over the premolars and first and second molars. In anthropoids, on the other hand, the maxillary sinus distends the jaw over all the premolar and molar teeth. It will be thus seen that the peculiar distension of the nasal canal in the gorilla and chimpanzee is probably of the same nature as the distension of the inferior meatus in apes.

In man, too, the inferior meatus is developed in an inverse ratio to the maxillary sinus. If one is large, the other is small; by the growth of both, by more of one than of the other, the requisite expansion of the superior maxilla is obtained in the adult. In

negroes and negroid races, an expansion of the inferior meatus at the expense of the maxillary sinus, if not the rule, is very frequent; such a condition or relationship as is shown in fig. 3, A, is common in these races. A vertical section of the face, made so as to sink through the nasal canal and emerge at the first molar, shows that the maxillary sinus extends only slightly over the premolar teeth, and that a line drawn from the centre of the first molar tooth to the nasal canal passes through the inferior meatus. In the commoner type of European skull, such a line passes through the maxillary sinus or its inner wall, and the antrum extends forwards in the jaw as far as the canine tooth (fig. 3, B). It will be thus seen that a development or expansion of the inferior meatus as a factor in the growth of the jaw and face, when such expansion (*i.e.*, growth) replaces

FIG. 3.—Contracted forms of inferior meatus and maxillary antrum or sinus. A, in which the antrum is small and inferior meatus large. B, in which the antrum is large and meatus small.

in part the function of an antrum, is to be regarded as a primitive or atavistic feature.

It is difficult to explain the curious distension of the nasal canal within the maxillary antrum in gorillas and chimpanzees. One feature has to be remembered: the air-sinuses of the skull and the laryngeal sacs, all diverticula of the respiratory tract, never cease growing as long as the animal lives; the older the anthropoid, the larger its air-sinuses. Their late expansion is evidently due to the pressure of the respiratory current, but why it should occur in the gorilla and not in the orang, if the cause is purely physical, is hard to explain.

There was no feature of the body that suggested more forcibly than the arrangement of the air-sinuses of the skull that the gorilla and chimpanzee were more closely related to man than either the

orang or gibbon. In apes, the growth of the face was accompanied by a distension of the inferior meatus and a growth of the maxillary sinus; in the gibbon and orang, the maxillary sinus attained an enormous expansion, and the sphenoidal sinus was also present and well developed. But in only man, the chimpanzee and gorilla was a frontal sinus, and one, two or three ethmoidal sinuses present, in addition to those present in the orang and gibbon.

(2) *The Musculature of the Bladder and Urethra.* By F. WOOD JONES, London Hospital, E.

It is not intended in this preliminary notice of the arrangement of the muscular coats of the urinary tract to lay claim to the establishment of any new facts, but it is claimed that by a careful study of sections of the foetal urogenital tract some light can be thrown on certain questions on which there is at the present day a considerable difference of opinion, and hence a considerable degree of doubt.

The subject has been carefully investigated by many observers both on the continent and in England, and the conclusions which have been arrived at vary widely. On the whole, these observations recorded from a study of the foetal sections agree in all essential points with the previously recorded observation of the continental observers, and so in a certain measure depart from the generally accepted account as current in the English text-books.

The method employed in this investigation consists of cutting sections that shall be large enough to show the anatomical connection of the parts, and at the same time thin enough to allow of their histological constitution being determined by the microscope.

The foetal material so far employed, for which, as well as for references to literature, I am indebted to the kindness of Dr Arthur Keith, consists of 2 ♂ of the 5th and 9th month, and 3 ♀ of the 4th, 7th and 9th month. Sections through the entire thickness of the pelvis in an antero-posterior direction, and extending to a little distance on either side of the middle line, were prepared, stained with logwood and eosin, and mounted.

The conclusions arrived at from the study of these sections have so far been confined to the three points—

(1) The arrangement and number of the muscular coats of the bladder.

(2) The situation and the nature of the sphincter of the bladder.

(3) The constitutions and arrangement of the muscular layers of the prostatic and membranous portions of the urethra.

With regard to the arrangement of the fibres constituting the musculature of the bladder wall, and the number of layers into which they naturally divide themselves, a good deal of difference of opinion exists. In the literature of the subject there are two main opinions held: on the one hand, it is asserted by some that three layers of muscular fibres can be uniformly traced, whilst others hold that two layers alone constitute the thickness of the bladder wall.

The conclusions arrived at are, that in these sections the muscles of



FIG. 1.—Photograph of a section—one of a series of fourteen—taken through the pelvis of a ♂ of 9 months.

It shows the bladder and prostatic urethra and part of the penile urethra in median section, and the other portions of the urinary tract somewhat off the middle line. It shows well the layer of muscular fibres connecting the rectum and the bulb.

the bladder wall are very definite and constant in position. They are seen to compose two complete, well marked, differentiated coats, and one coat which, though incomplete, is well marked and well differentiated.

The two complete coats are (1) the external longitudinal and (2) the immediately underlying circular.

(1) The external longitudinal layer consists of fibres below and in front in (a) fibres which arise from the pubis, and which constitute the pubo-prostatic ligament, and which arise around the neck of the bladder by dipping to a certain extent interlacing with the circular layer.

The fibres from these two sources sweep upward to the extent of the bladder, and are continued unbroken down the wall. Here they are inserted (a) by interlacing with the fibres of the circular layer, and (b) by becoming fixed to the prostate, and in the female to the anterior wall. This coat therefore forms an unbroken coat to the bladder.

(2) The middle circular layer consists of well marked bundles of fibres that extend over the entire bladder in front and behind. These coarse bundles of muscle fibres in the fourth and fifth months are not differentiated from the longitudinal layer, but, massed around the neck of the bladder, constitute the proper sphincter. But in foetuses of the full term they are by their arrangement well marked off histologically from the longitudinal layer, and actually enter into the formation of the sphincter.

(3) The third layer of the bladder is incomplete. Its fibres are longitudinal, and it exists only on the anterior wall of the bladder, where it forms a well marked thickening up the anterior wall, and extends only to the top of the bladder in most specimens; and in those cases in which it extends to the posterior wall, it does not reach far down, never reaching the trigone, and almost always losing itself before it reaches the neck. Below and in front it sweeps over the heaped up sphincter of the neck, and is directly continuous with the longitudinal layer that lines the urethra.

It will be seen that by this arrangement only longitudinal muscular fibres exist in the trigone—the outer longitudinal layer is thickened—and in older specimens differentiated into a circular layer. With regard to the proper sphincter, these specimens uniformly and definitely show that the fibres of the neck of the bladder are arranged in such a manner that a well developed and differentiated sphincter is formed.

In the foetuses of the 4th and 5th months the circular layer of the bladder as it approaches the neck becomes thicker, and the neck is heaped up into a definite sphincter, this heaping up being better marked behind than before; while in the full term foetuses, the sphincter is not only marked off as a distinct muscular layer, but also as differentiated fibres that are distinct from the rest of the muscle bundles of the circular layer.

The coarse and loosely packed bundles of the circular layer change with some suddenness, and give place to the finer and more distinct and more closely packed fibres that are proper to the sphincter. These peculiar fibres extend behind up to the trigone.

With regard to the musculature of the urethra, the foetus of 4th or 5th months shows no differentiation, and the foetus of 9 months only slight differentiation between striated and non-striated muscular layers.

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FIG. 2.—Semidiagrammatic section of ♀ urinary tract at 9th month.

the muscles into voluntary and involuntary layers is marked rather by slight hiatus existing between the two layers than by any well marked histological distinction separating the one from the other.

The musculature consists down the entire pelvic aspect of the urethra, as far as the meeting of the corpora cavernosa, of two layers of fibres—an outer circular and an inner longitudinal. Both these layers are directly continuous with the corresponding layers of the bladder, the inner longitudinal fibres streaming unbroken over the sphincter of the neck of the bladder and up its anterior wall, the outer

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continued downwards unbroken throughout the membranous to the bulbous urethra.

The outer circular layer is simplest in the female, and on the posterior wall exists in exactly a similar condition to the same layer on the anterior wall; that is to say, consists of an unbroken layer, continuous definitely and directly with the circular fibres of the bladder.

But in the male, after the fibres have passed below the sphincter of the neck, they are broken up—as is clearly shown by the male sections of different ages—by the outgrowing tubules of the prostate. These tubules, budding out from the posterior wall of the urethra, carry out before them the circular layer of the urethra, and scattering the fibres before them in all directions, push the muscular layer of the urethra before them so that the prostate becomes covered by a muscular layer that was originally the circular layer of the urethra.

Outside the two layers, longitudinal and circular, that compose the involuntary sphincter of the urethra, the fibres of the voluntary sphincter are seen marked off from them by a hiatus rather than by well marked histological distinctions in the fibres,—the distinction between striated and unstriated muscular fibres in the urethra being evidently post-natal.

This voluntary sphincter of the urethra consists, not of a flat muscular plane, but a cylindrical layer of circular fibres extending over the lower prostatic and the membranous portions of the urethra. In no specimens is the triangular ligament seen.

These muscular strata compose the proper musculature of the membranous and prostatic urethra, but in addition to this, the lower part of the membranous and the bulbous portions of the urethra in the male receive a curious addition of fibres. These fibres pass in a broad sheet from the anterior surface of the rectum, and compose a thick plane of muscular tissue connecting the anterior longitudinal coat of the rectum and the posterior wall of the membranous and bulbous portions of the urethra,—the fibres intermingling with the circular fibres of the urethra and the muscles of the bulb.

(3) *Recent Observations on the Human Stratum Corneum.*

By Dr J. M. H. MACLEOD.

The stratum corneum is the part of the skin which we see and feel, and in which we can actually watch pathological processes.

Among the many difficult problems which present themselves in the histo-pathology of the skin there are perhaps none which are more pertinent in the present state of our knowledge than those concerning the various abnormalities in the process of cornification.

The ordinary text-book descriptions of the horny layer are wholly inadequate to explain *several important facts* such as—

- (a) Why the skin forms a waterproof coating to the body, through which water and substances dissolved in it cannot penetrate.

- (b) The reason of the initial difficulty in cutting or piercing the skin.
- (c) Its power of resisting mechanical injuries.
- (d) Its power of preventing the entrance of micro-organisms and their toxins.

It is customary to regard the st. corneum *as a degenerate structure*. In reality it is a *highly evolved structure*, and only its superficial cells, which are subjected to friction, pressure and drying, are useless and degenerate, whereas the cells of the deeper layers give to the skin the four characteristics referred to.

A *perfect horn-cell*, such as occurs in the deeper part of the st. corneum of the palm of the hand and sole of the foot, is large, faceted from pressure, flat and elongated in shape. The *nucleus* has either completely disappeared, or remains as a shrivelled mass of debris situated in a space in the centre of the cell. The *spongioplasm* of the cell may still be detected forming a fine network, in the meshes of which the *hyaloplasm* has been replaced by a *fatty or waxy substance* which stains with osmic acid. The cells are closely pressed together, and the inter-epithelial lymphatics can no longer be detected. The keratohyalin and eleidine of the transitional layers have disappeared.

This fatty substance like beeswax is present throughout the st. corneum, but is in greater quantity in the deeper layers. It is to it that the *waterproof character* of the skin is due.

The cells have undergone another change—they have become keratinised. Part of the cell has become transformed into the highly resistant substance known as *keratin*, which resists the action of 50 per cent. mineral acids and is indigestible in pepsin-hydrochloric acid.

The origin of the keratin is still a subject for controversy. At one time it was believed that the whole cell became transformed into keratin; at another it was suggested that only the spongioplasm became keratinised; and a third view was that keratin was produced by an alteration in the intercellular substance. The publication of the digestion experiments of Unna marked a distinct advance in our knowledge of the cornification-process. These experiments I repeated in a modified form, first in Unna's laboratory four years ago, and intermittently since then.

Transverse and vertical sections of the st. corneum were digested for twelve hours at 40° C. in the following solution:—

Pepsin,	0.5
Hydrochloric acid,	1
Water,	100

After digestion the sections were hardened for a few minutes in absolute alcohol, washed and stained. On microscopical examination it was found that they presented the appearance of a fine network like a honeycomb, the contents of which had completely gone. The periphery of the cell alone resisted the action of the pepsin and had become keratinised.

A series of experiments were also done by *macerating* the horn-cells. For this purpose salicylic acid, glacial acetic acid, and peroxide of hydrogen were found to be the most serviceable macerating fluids. After immersing a piece of skin from twelve to twenty-four hours in one of these fluids, a pulp of cells could be scraped off from the stratum corneum and stained and examined on a slide, or first digested and then examined, when the separated cells appeared like little faceted shells.

Stained macerated horn-cells showed the presence of numerous fine granules on the surface. These granules have given rise to considerable discussion. Raush believed them to be outside the cells. Ernst thought that they were keratin granules and inside the cells, and Kromayer stated that they were artificial products of the staining.

A prolonged series of experiments led me to regard them as keratin. They seemed to be on the surface of the cells; towards the periphery they were shaped like spicules, while near the centre of the cell they were round specks; they appeared to be prickles in "relief."

The following were the reasons which induced me to regard them as keratin bodies on the surface of the cell, and probably as keratinised prickles:—

(1) They resisted mineral acids and pepsin-hydrochloric acid like keratin.

(2) They stained like keratin.

(3) By the staining methods employed there was little or no precipitation, and thymol was added to the macerating fluid to prevent the occurrence of bacteria, with which the granules might have been confounded.

(4) The "granules" were grouped as if they belonged to individual cells, and not diffusely spread like a precipitate.

(5) The prickle-cells of the Malpighian layer present a similar appearance when the prickles are seen in relief.

Cornification thus consists of the transformation of the inter-epithelial fibres and probably the outer part of the intra-cellular spongioplasm into keratin. This would seem to be brought about by an inherent power of the fibres themselves.

Keratohyalin is not a previous condition of keratin, as is generally taught. It is a separative product of the protoplasm of the cells. Eleidine is a further change in keratohyalin, and fat is most probably the ultimate result. Keratohyalin and eleidine are merely accessory, and not essential to the process.

The horn-cells are closely welded together by their keratin-spicules; within they have fat. In this way the layer forms a varnish for the skin, and its power of resistance is explained.

Mr N. BISHOP HARMAN pointed out that there were substances other than fat which appeared to be stained by the application of osmic acid. This is found particularly in compressed tissues.

In recent staining of sections of the epidermis for micro-organisms,

nothing had impressed him so much as the way the keratin granules were picked out by Gram's method. The rete malpighii in its deepest layer was practically free of retained stain, the upper layers began to show stained granules, the stratum granulosum was full of deeply stained granules, this staining became deeper, and more widespread in higher layers, until the stratum corneum appeared as deeply stained plates.

He felt that these appearances warranted the present conception that the cells of the rete malpighii secreted a material which permeated the cells of the epidermis, converting the upper layers into simple protective horny squames, and were against any suggestion of a fatty change or combination. Any fat present in the scarf skin he thought was likely to be the secretion of the proper lubricators of the scarf skin, the sebaceous glands.

(4) The description of the museum preparations and the specimen exhibiting a cervical rib on each side, shown by Dr C. ADDISON, will be published in the next number of the *Proceedings*.

(5) Dr H. W. MARETT TIMS gave a paper "on the Succession of the Molar and Premolar teeth in the Mammalia." A full account of this communication will appear in the July number of the *Journal of Anatomy and Physiology*.

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